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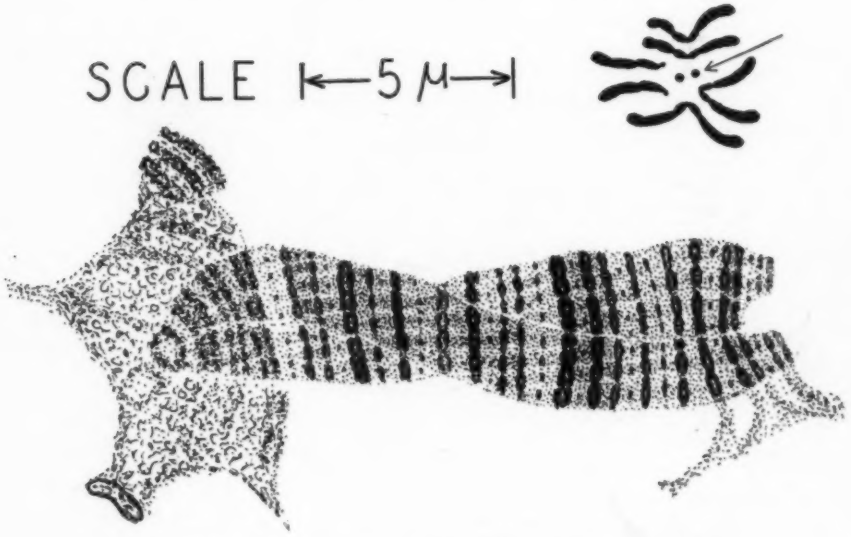

"NORMAL" AND GIANT CHROMOSOMES COMPARED

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Early Maize Genetics

Color Inheritance in Cattle

Three More Generations of Toothless Men

Population in America and Japan

A Dwarf Mutation in the Rat

VOLUME 26 FEBRUARY, 1935 NUMBER 2

The American Genetic Association

An incorporated organization devoted to promoting a knowledge of the laws of heredity and their application to the improvement of plants, animals, and human racial stocks

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COMING

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More Hair Variations

The series of parallel mutations in men, swine, and cattle published last year has aroused much interest. Now the rodents are coming into line with two "negroid" hair mutations quite similar in appearance to the others in the series.

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Variations in Barley

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Recent Birth Rate Trends

Is the long decline in the European birth rate about at an end and are replacement size families likely to be more common in the future?

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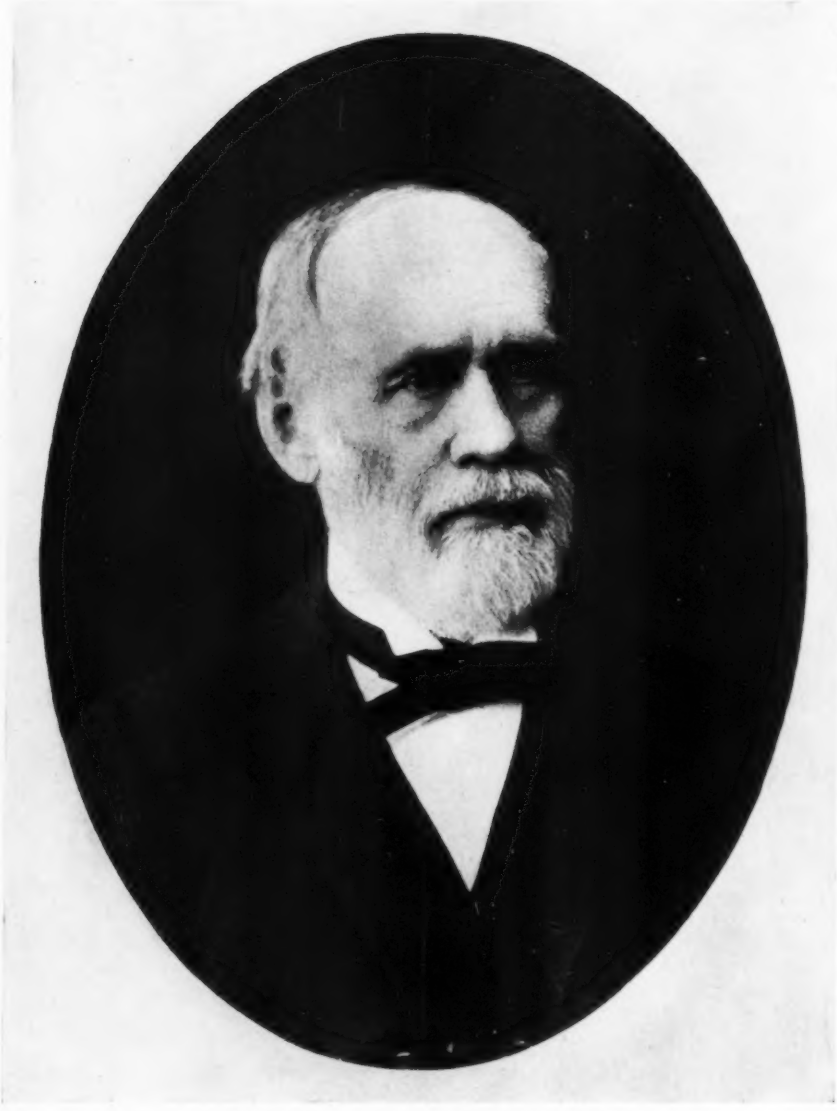


THE FIRST SCIENTIFIC MAIZE BREEDER

Frontispiece

Professor William James Beal, of Michigan Agricultural College, was the first to advocate pollen selection in maize improvement and the first to hybridize maize for the sole purpose of increasing the yield of plants grown from crossed seed. He pointed out that selection of the male parent was of prime importance. Utilization of hybrid vigor by the modern method of crossing selected inbred lines is a logical development of the crossing of varieties practiced by Professor Beal. His work with corn began about 1870, thirty years before the rediscovery of Mendel's Laws.

EARLY RESEARCHES IN MAIZE GENETICS

W. RALPH SINGLETON
Connecticut Agricultural Experiment Station

SOON after agricultural research was officially begun in the United States with the founding of the experiment stations (the first was the Connecticut Station, 1875) several experiments were carried on in an attempt to improve the maize plant by hybridization and selection. Indian Maize (*Zea mays* L.) had long been the leading agricultural crop of the North American continent when the white man first set foot here, and certain of the Colonial fathers were interested in its improvement. The coming of the experiment stations, however, assured a proper environment for research on the maize plant.

Because of this interest in corn, there were many excellent observations on its culture and improvement before the laws of heredity were formulated. All of these experiments were recorded in scattered publications. We are attempting here to bring together the most important of these and weigh their significance. Some workers merely accumulated masses of data which they interpreted to support their preconceived notions of how inheritance should work. Other investigators made real progress and marked milestones on the road of knowledge.

The earliest investigations of corn were concerned with pollination. Would corn pollen of one sort affect in any way the fertilized seed of another kind? This was a warmly debated topic in those days.

Early Experiments

Camerarius in 1694 proved that the pollen of maize is necessary for fertilization of the ovules (Roberts[27]*). Zirkle[35] has shown that some of the early American colonists in the first half of the eighteenth century, especially Cotton Mather, Paul Dudley, and James Logan, were vitally interested in Indian corn and carried on experiments demonstrating that the maize pollen fertilized the ovules. Roberts[27] pointed out that in the first half of the nineteenth century, Lecoq and Gärtner hybridized maize. Gärtner made several crosses, but did not isolate or self-pollinate the F_1 plants and so his experiments on maize are of little value. Vilmorin in 1867 (according to Webber[34]), planned an interesting experiment to test the immediate effect of pollen when applied to other varieties of corn. In the spring he planted several varieties about 1,000 feet apart, which distance had been found sufficient to prevent intercrossing by wind-blown pollen. The ears to be crossed were wrapped in thin flannel, which excluded foreign pollen. Such ears unless pollinated produced no kernels. As a check, one ear of each variety was pollinated by pollen of the same plot. The ears thus obtained were imperfectly filled, but the kernels were all true to the type of the race. On the other hand, when ears were artificially pollinated with pollen of another sort, the ears often, but not always, contained kernels showing the characters of the male parent. The proportions obtained were inconstant, varying from 1 to 60 per cent of crossed grains. The effect was limited to changes in color of the kernels, in most cases the pollen used being from a black ear.

Before 1870 Hildebrand[14] also made some experiments in corn pollination. He selfed some ears and obtained seeds all like those planted. Then he at the same time made some cross pollinations. He used a yellowish race as the female and a dark brown race as the

*Numbered references are to Literature Cited, which will appear at the end of the article in the March issue of the *Journal*.

male parent. This dark brown color must have been a pericarp color but he also had aleurone color under the pericarp, as is shown by his results. The color could also have been produced by the interaction of two complementary factors. He pollinated some of the yellow ears with their own pollen and obtained all yellow ears. He pollinated two yellow ears by pollen of the dark brown race. These had about half the kernels yellow, like the female parent, and remainder a dirty violet color. He concluded that the pollen of the brown-kerneled sort had exercised a direct influence on these. His work was criticized by Körnicke who stated that the color was in the pericarp and that it could not be transmitted to other ears the first year (see Webber[34]). Körnicke was right. Hildebrand's observations were undoubtedly correct too. What Körnicke did not realize was that there was *aleurone* color as well as pericarp color in the brown corn and the aleurone color was the one transmitted. Körnicke grew two fields of Early Yellow Baden corn in 1871. One was left to be open-pollinated by its own pollen. It came true to seed. In the second field, some of the ears were pollinated with pollen of the reddish-black maize, the color of which was in the pericarp and in the aleurone layer. The cross pollinated ears developed yellowish-red and dark red kernels and also kernels like those of the mother race.

Focke,[10] used the term "xenia" to denote immediate influence of pollen of another race on any tissue except the hybrid embryo. He found xenia when white or yellow maize was pollinated with pollen of brown or blue seeded maize. No xenia was found in the reciprocal pollination or when yellow was pollinated by yellow or when smooth (starchy) maize was pollinated by wrinkled (sugary) maize. Darwin[7] showed experimentally that cross-fertilized maize plants were taller than corresponding self-fertilized plants. He also cited[8] an experiment of a Dr. Savi, who in 1816 sowed yellow and black seeded maize together and on one ear some of the seeds were yellow, some black and some mottled.

T. J. Burrill, in 1877, conducted an experiment from which he concluded that pollen of one sort may exert an immediate influence on the endosperm of another kind. Similar conclusions were reached by W. W. Tracy in 1888. (Both of these citations are from Kellerman and Swingle.[19])

William James Beal, Professor of Botany at Michigan Agricultural College (1870-1910), was the earliest to consider scientifically the improvement of maize. He was a real leader in whom were combined the rare qualities of clear thinking, keen observation and initiative. He showed how foolish was the then-prevailing policy of selecting ears only. Pollen should be selected as well. Also, he was the first to hybridize corn for the sole purpose of increasing the yield of plants grown from the crossed seed. His story is best told in his own words (Beal[1]):

> From all that I can learn of others, and from my own experiments, I am fully convinced that there is as much chance to use skill in crossbreeding plants (as in breeding animals). *This crossing of plants by human agency is yet in its infancy, but I anticipate in the future great improvements in this direction in our wheat, oats, corn, garden vegetables, in our orchard and garden fruits and in our ornamental plants.**
>
> Here are some ears of pop corn which grew in the vicinity of some sweet corn. A few grains of pollen here and there changed the color, size and texture of some of these kernels. The male element has produced a remarkable effect the first year. With all kinds of plants the effect is not so apparent on the first year, *but the quality of the pollen in all cases should be looked after to secure the improvement of varieties.**
>
> What do we think of a man who selects the best calves, pigs, and lambs from the best mothers, paying no attention whatever to the selection of a good male parent? This is what our very best farmers are now doing all the time with their seeds and plants. They select from a field the largest and fairest ears of corn and the plumpest wheat.
>
> In our corn fields are often large numbers

*Italics ours.

of slender stalks, bearing no ears, or very small ears. These stalks have tassels, and they scatter pollen and are very apt to scatter some on the ears of the best stalks,—on the very ears which we shall select for seed. The different kernels on the same ear may have twenty or more different male parents. Now theory and analogy at least tell us, if we wish to improve our corn to the greatest extent, we must pay some attention to the pollen used. A much better way would be to plant a piece of corn by itself on good soil and treat it well, giving the stalks plenty of room. Before shedding pollen, cut out entirely or remove the tassels of all the poorest stalks. In this way, we not only select seed from good females, but also from those fertilized by good males. Wheat, oats, rye, barley appear to be self-fertilized before the flowers open. I have already referred to their improvement.

Here we have the first disciple of pollen selection in maize breeding. His statement concerning the rôle to be played by hybridization in plant improvement is indeed prophetic. Later in a talk given at Charlotte and Flint, Michigan Farmers' Institutes in January, 1878, Professor Beal[2] elaborated somewhat on the method of seed corn production and gave the results of his own experiment in crossing flint and dent corn. His statement is as follows:

Before leaving this subject I want to show you some corn which is the result of this experiment. In the spring of 1877 I planted a small piece of a small, early, eight-rowed, Yellow-Dent corn, called Yankee or Jersey Dent. In the midst of this piece I planted a single row of smutnose, Yellow Flint corn. Before flowering, the tassels of the Flint corn were carefully and thoroughly removed. The Flint corn was a trifle earlier than the Dent so the fertilization of the Flint corn was imperfect. There was scarcely a full ear in the lot, but all that there was looked just like Flint corn. There was no sign of any cross with the Dent. This Flint corn, which I know was crossed, was planted by itself this summer, and here I show you some of the ears. There are all grades, from what looks like pure Yankee Dent corn. The pollen or male element produces a marked effect and should be attended to.

This last observation is not true of our first generation flint-dent hybrids when a large Leaming (12-18 rows) is used as one parent. Beal, however, crossed an eight-rowed dent with a flint. As both parents were eight-rowed, the differences he mentions were probably in kernel types.

The Farmers' Institutes in Michigan, as in most states, were held each winter in practically every county. They preceded the present Extension service. Professor Beal always spoke at some of the meetings. As corn breeding was one of his hobbies, we can find notes on this subject in almost any of the Farmers' Institute reports, published with the Michigan State Board of Agriculture reports. We now quote from the 1880 Report of the Board of Agriculture.[3] This address was delivered in January, 1880, at different Farm Institutes.

Will pollen show its effect on the first year in crossing two kinds of corn?

It is generally stated that it will. On this point I have made some experiments. In 1879 I planted in my garden near each other, three hills of the following kinds of corn, well mixed together, viz: Waushakum, (a yellow flint), white flint, black pop corn, early Minnesota sweet, black sugar, and a very dark King Phillip. Every ear showed a sign of mixture by pollen from one or more of the other varieties, except those of the King Phillip; perhaps there was even here some change in the texture of the kernel, but I did not preceive it. Dr. Sturtevant, in the Report of Connecticut Board of Agriculture of 1878, says: "The red corn presents a fixity of type which overcomes, in most instances, the effect of crossing even in its color." He says a careful examination shows a change in the shape and quality of the kernel.

Climate has a wonderful effect on corn. Professor Shelton of Kansas Agricultural College sends corn to the Michigan Agricultural College which has been raised there for three years. It went to Kansas as King Phillip, it comes back well marked with dent. He says it is the effect of the climate and is not due to crossing with dent corn.

We see here that humor is not lacking in Professor Beal. Kansas may have an exceptional climate but it is hardly conceivable, as Beal knew, that flint corn could be changed into a flint-dent hybrid by climate alone.

A very careful experiment to test the yield of crossed corn in comparison with standard varieties was outlined by Professor Beal in this address. It had been previously published in the *Farmers' Review*. This seems to us the first attempt by anyone to cross corn with the sole purpose of increasing the yield. Five investigators were to cooperate in this experiment.

Each man in his own State shall select two lots of seed corn, which are essentially alike in all respects. One should have been grown at least for five years (better ten years or more) in one neighborhood, and the other in another neighborhood about 100 miles distant. In alternate rows plant the kernels taken from one or two ears of each lot. Before plowing, thin out all poor or inferior stalks. As soon as the tassels begin to show themselves in all the rows of one lot, pull them out, that all the kernels on the ears of those rows may certainly be crossed by pollen from the other rows. Save seeds thus crossed to plant the next year by the side of seeds of each parent. Seeds of one parent can be obtained from the rows not topped. Seeds of the other parent should be planted by themselves to get pure seeds of the same year.

The next year the crossed seed was to be grown in comparison with the varietal seed.

A similar experiment was made at the Agricultural College in 1878. In this the advantage shown by the crossing of corn over that not crossed was as 151 exceeds 100, and in the case of black wax beans it was as 236 exceeds 100. In a similar experiment made during the past two years at the Agricultural College the corn from seed of crossed stock exceeded that not so crossed as 109.67 exceeds 100, or nearly ten per cent in favor of crossed stock. The experiment was quite carefully made and I do not consider this result as purely accidental.

The results of this cooperative experiment were published a year later.[1] It succeeded as well as many cooperative enterprises. Three of the investigators did not complete the experiment. One planted the corn but failed to report. Beal secured two varieties of white Flint, one from Oakland (grown ten years there), and one from Allegan County (grown six years).

In spring of 1882 three rows of crossed seed were grown in comparison with Oakland Flint. Pure seed gave 57½ pounds and crossed seed 69½ pounds of ears per plot, or about 21 per cent more from crossed seed.

Not all of the early investigators of corn were as careful observers as Professor Beal of Michigan. In the First Annual Report of the Ohio Experiment Station, in 1882, there is an outline of an experiment by Professor William R. Lazenby[22] to test corn crossing. Eight different plots of three rows each were planted and the center row was detasseled in each case. The order of planting in the eight different plots was as follows:

Plot 1	Flint	— Dent	— Flint
Plot 2	Dent	— Flint	— Dent
Plot 3	Dent	— Sweet	— Dent
Plot 4	Sweet	— Dent	— Sweet
Plot 5	Flint	— Sweet	— Flint
Plot 6	Sweet	— Flint	— Sweet
Plot 7	Red	— White	— Red
Plot 8	White	— Red	— White

The conclusions were:

In scarcely a single instance was the effect of the cross shown, and in no instance was the change more marked than that seen when the variety was planted by itself. The Flint corn was to all appearance pure Flint and the Dent pure Dent. *The Sweet Corn was also unchanged.** Even the red and white varieties preserved their respective colors with very slight modification. It appeared almost certain from the results of these tests that the changes seen, excepting, perhaps, size and quality of ear, were the results of cross fertilization of previous years.

No influence of the pollen should have been expected in any of the various flint-dent combinations, even when red and white varieties of corn were crossed. The red color is in the pericarp and does not show up until the next generation. But there should have been some influence of the starchy pollen on sweet ears. Why this was not observed is not known. Surely sweet corn pollinated by either flint or dent does not have the appearance of sweet corn. If all the tassels of the sweet corn were removed, there must have been starchy kernels on the sweet ears, although not observed by the investigator. In a later report of this same cross he contradicts his former statement.[23]

Flint on Sweet (Cross of '82)

This cross was quite successfully accomplished and some well developed ears were secured. The Flint variety seemed to exercise a very strong influence on the product the first year.

The rows, shape of ear and arrangement of kernels was that of the female parent, but the kernels were, with but few exceptions, filled up full at the points like Flint.

This corn was planted, like previous crosses, in a plot by itself in the spring of 1883. The product is about two-thirds white and yellow Flint kernels and one-third Sweet corn kernels. The arrangement of the rows and ker-

*Italics ours.

nels is more that of Flint than Sweet Corn.

This statement more closely agrees with what undoubtedly occurred than the former. Here was an excellent opportunity to get the exact ratios of starchy to sweet kernels, also yellow to white, had the counts been made. The corn was grown in an isolated plot and all the ears were either selfed or sib pollinated.

Apparently no count was made for none was mentioned. The estimated number of two-thirds *Su* to one-third *su* varies considerably from the 3:1 ratio that could have been obtained had the kernels been counted.

In a cross of sweet on flint the product of the cross showed one-fifth sweet corn and four-fifths flint kernels. Here was another approximation of a 3:1 ratio. Possibly the small percentage of sweet kernels is accounted for by the fact that some of the Flint seed planted had not been crossed by sweet and hence there would be an excess of Flint pollen in this isolation plot.

Not much significance was attached to the pollination of sweet corn by flint or the reciprocal pollination. In 1885, Lazenby makes the following statement "From many tests, conducted specially to investigate this point, the conclusion is reached that well established varieties do not show the effect of cross-fertilization the first year to any appreciable extent."

First Observations on Linkage

Seventeen years before the rediscovery of Mendel's law, association of two characters in heredity was observed by Dr. E. Lewis Sturtevant,[31] first Director of the New York Agricultural Experiment Station at Geneva, New York. The characters under observation were tunicate and starchy. His account is as follows:

In 1882 we received a small package of seed of the pod corn from Professor W. J. Beal, of Lansing, Michigan. This seed was all podded, and when freed from its husk was all of uniform type, a yellow dent. Planted in the Station garden it furnished us with a number of ears, some fastigiate, others heavily husked, others lightly husked, and some free from husk. Some of the unhusked ears were red-kernelled, the only mixture being kernels of red sweet; other had white, yellow and ordinary amber sweet kernels. During the growth we noticed that wherever, a plant was bearing the typal form of husked grain the tassels were heavy, branchy, and usually bore more or less podded kernels.

*In no case were sweet kernels found in the podded ears examined, although sweet kernels were abundant on the unpodded.**

The corn grown by Sturtevant must have been previously crossed by sweet. It probably was of the following genetic constitution: $\frac{su\ +}{+\ Tu} \times ++$ a tunicate starchy ear having been crossed with sweet normal pollen two years before and the progeny back-crossed by normal starchy pollen. This seems plausible since the tunicate corn was probably originally starchy and it would be an easy matter for a tunicate ear to be pollinated with sweet pollen. This segregating ear must have been pollinated by starchy pollen since there were no sweet grains on it. Of course there was the possibility that the segregating plant could receive its own pollen. If it received it in any appreciable amount there should have been some sweet grains on the ear. We know that a plant growing in a field of corn will receive very little of its own pollen, not more than five or ten per cent. The ear received from Beal had only starchy kernels, showing it had received only *Su* pollen. With perfect linkage then there would be but two classes of ears in the crop grown by Sturtevant, $\frac{su\ +}{++}$ (normal ear and segregating sugary) and $\frac{+\ Tu}{++}$ (all starchy ears and all Tunicate). The linkage however is not perfect: there is 28.6 per cent crossing over. Had Sturtevant examined enough Tunicate ears and enough kernels on each he would undoubtedly have found some sweet kernels. And surely there were some normal ears that were homozygous *Su*. Although Sturtevant

*Italics ours.

probably did not examine enough ears to obtain all the facts it is interesting that he observed this association between starchy and tunicate long before a Mendelian ratio was established in maize.

Sturtevant[32] grew a great many varieties of all the races of corn, dent, flint, sweet, pop and soft in close proximity and made observations on the amount of crossing among the different varieties and races. From these he drew conclusions that he stated in ten propositions:

Proposition 1. Under the conditions of ordinary seed, maize does not in general show the effects of current cross-fertilization, the exception being the sweet corns, which exhibit the influence of current foreign pollen very readily.

Proposition 2. The agricultural species of corn have a strong tendency to resist cross-fertilization with each other, the average resistance in our trials being 66 per cent success; 34 per cent failure.

Proposition 3. Cross-bred corn has a greater tendency to current cross-fertilization than purely bred corn, on the face of our evidence.

Proposition 4. There is a resistance to current hybridization between the races of a species.

Proposition 5. Current cross-fertilization is facile between varieties of the same race.

Proposition 6. Where cross-fertilization has taken place in maize, the tendency is to produce both parental types, and not toward intermediates.

Proposition 7. Color can pass, through current hybridization, very freely from one agricultural species to another.

Proposition 8. Red color is the strongest of the colors in resisting the action of current hybridization, yet it is by no means insensible to the action of proper pollen.

Proposition 9. Kernels can be partially fertilized by several kinds of pollen.

Proposition 10. Sports in a crop from hybridized seed are not common.

We can see that not all of his propositions will stand today. His first proposition showed fairly good observation, although he should have noted yellow kernels on white ears and colored kernels on both yellow and white ears. His second proposition was probably not justified, although selective fertilization in favor of the plant's own pollen has been demonstrated by Jones[17] in pollen mixtures. Sturtevant's facts were true for Proposition 3, but his interpretation wrong. The cross-bred ears were merely segregating. Proposition 4 was probably not justified. Proposition 5 is of course correct. His facts did not justify Proposition 6, since he was speaking mainly of variety characteristics such as row number and flint and dent kernels. He secured many intermediates. Proposition 6 is of course true for kernel characters. Proposition 7 is true. Proposition 8 is true, since the red color is in the pericarp and is not affected by pollination. He did not examine the kernels to find where the color was located. Proposition 9 we know is not true today, although the embryo and endosperm may be fertilized by different pollen grains. His facts probably justified Proposition 10.

Here was apparently the first attempt to formulate any laws concerning heredity in maize. Sturtevant's observations were made on open pollinated stock. He showed fairly good observation in some cases but in other instances stretched his data to fit his belief, a not uncommon occurrence in research work. Nevertheless his ten propositions probably served as a stimulus to other workers and in that way served a useful purpose.

The Kansas Studies

The first really intensive study of hybrids of maize was made by Kellerman and Swingle[18] at the Kansas Experiment Station, Manhattan, Kansas. They made a great many hybrids, many of them between varieties of maize which should have given excellent segregations in the second generation. The results of these investigations were published in the first and second annual reports of that Experiment Station (1888 and 1889), also in Bulletins 17 and 27. Some of these were crosses between yellow and white, starchy and sweet, and red cob versus white cob. These ratios were overlooked in their zeal to make all hybrids the "blends" of the two parents.

They used closely woven cloth sacks for both tassel and ear bags. The first year 66 cross-fertilizations were attempted, 39 of which were successful. They also attempted self-fertilization by

E. LEWIS STURTEVANT

Figure 1

In 1883 Professor Sturtevant reported the fact that the characters tunicate and sugary tended to be associated in inheritance. It is now known that these characters are linked, with a crossover value of 28.6. Sturtevant's observations antedated the rediscovery of Mendel's Law by seventeen years and the discovery of "coupling" and "repulsion" in peas by Bateson and Punnett by 21 years.

building cages around individual corn plants before pollen was shed. The cages were constructed one-half of wood and one-half of cotton cloth. The top was cotton. A window sash was inserted in one of the wooden sides. No selfed seed was obtained on any plant. Neither was seed obtained when one of the plants was pollinated by other corn pollen. So they concluded the experiment worthless. The following year,[19] 188 crosses were attempted, of which 175, or 93 per cent, were successful. Also in 1889, the seeds of the corn crossed in 1888 were planted adjacent to each other, the plots being arranged so that pollen of adjacent plots would mature at different times, thus avoiding pollen contamination.

One cross, White Flat Ensilage × Landreth sugar, gave these results:

> Differs from White Flat Ensilage in that the ear consists of about *one-fourth sweet corn*, and the remaining kernels are more or less dented at the summit.*

In a cross, supposedly of Early Landreth Market × Early Golden Lenawee, the following results were obtained:

> Differs from Early Landreth Market in the large proportion (*probably* ¾) of yellow kernels, ...*

In a cross of Breck's Premier Sugar × Campton's Early seven-eighths of the kernels were flint (*Su*).

When Breck's Premier Sugar was crossed with Silver Lace pop, the resulting ears each had about ⅛ yellow, ⅛ sweet, and the rest like pop only larger. The ⅛ yellow must have been from contamination. The percentage of sweet kernels is only half of what it should be for a 3:1 ratio. This discrepancy might be caused by foreign pollen or it is possible that the pop corn was carrying the *Ga* factor which accelerates pollen tube growth. About 16 per cent of sweet kernels are found on ears segregating for *Ga ga* and *Su su* when the *Ga* and *su* are linked. The *Ga* factor is present in nearly all varieties of pop corn.

The investigators recognized two types of variation in the crossed corn grown the second year (F_1 plants), "I: in which the kernels on each ear were uniform, and II: in which the kernels were more or less variable; but a few numbers were intermediate." The latter ears were segregating for endosperm characters.

Their conclusion was:

> These results seem to suggest that when the effects of the cross are manifest the first year, the variation is more likely to be of type II the second year, but if they are not manifest, the variation to be expected is oftener of type I.

They present some very good illustrations of two ears segregating for starchy-sugary.

*Italics ours.

In 1890, they planted the seed of the corn crossed the previous year.[20] One hundred and twenty-one of the crosses were planted. "The seed germinated satisfactorily and the plants grew well until they were injured or killed by drought. Those not killed were injured to such an extent that scarcely a well-filled ear of large or normal size was obtained."

These investigators selfed or sib-pollinated two or three ears from each cross. These ears were described in detail. Of the 62 crosses harvested, 5 were too imperfect for comparison. Of the remaining 57, they state that 43 or 75 per cent showed evidence of the cross, that is, were intermediate (eight of them in color only) between the parental types. The crosses so described were all hybrids between various combinations of flint and dent varieties. No sweet varieties were used. Because of the poor character of the selfed ears, no valuable notes were obtained. There should have been opportunity to secure some ratios of yellow-white kernels had the ears been better developed, as there were several crosses of this nature, some in flint-dent hybrids, where the color is easily distinguished. Even in poorly developed ears they should have distinguished two different colors of kernels, although the proportions were not significant. This they failed to do. Kellerman and Swingle were the first to conduct such a large hybridizing experiment with maize and they had ample material to obtain first class 3:1 ratios. Of course, there is quite a gap between a 3:1 ratio and the interpretation of this ratio to mean that the independent determiners of heredity are assorting at random, that each has just an equal chance of being included in the gamete, and that one determiner is dominant over the other. But these investigators had three good characters to work with, yellow-white, starchy-sugary as endosperm characters, and the red-white cob color, had they counted enough plants to obtain a satisfactory ratio. It is true, they were working under difficulties. Almost every year they had a severe drought, which either killed the plants or severely injured them. Such conditions are not favorable to the formation of well-filled ears suitable for obtaining good ratios.

Kellerman and Swingle planted white sweet seed from a segregating ear and obtained two ears almost entirely sweet, there being no dent grains on one ear, while the other had but five to ten grains. From this result they concluded that sweet grains reproduce themselves much more exactly than did the dent grains from the same ear, a good observation.

We now quote from the summary:

> The effects of the crossing are in comparatively few cases (mostly in sweet varieties) visible the first year. The second year (or second generation) shows ears more or less completely blended, often exactly intermediate between the two parental types, more rarely the grains of a single ear are unlike each other, and each may resemble closely or remotely either parent. The product of the third year is generally true to the seed planted (as shown by the record of this year only) by selecting diverse grains from any ear, or from different ears, ears are obtained with grains usually like those planted. Any desired form of a 'cross' can therefore apparently be perpetuated.

This is enough to show they had the old-fashioned ideas regarding hybrids. They had considerable evidence of independent characters segregating but they considered these to be exceptions.

Before leaving these two early investigators it would be well to point out that the first genetic ratio ever actually counted and recorded on corn was reported in 1891 by Kellerman and Thompson.[21]

In the spring of 1891, Swingle, while assorting corn, noticed a few ears having blue kernels. He saved some of these for planting, "with a view to determine whether the blue was a sport, or the product of atavism, or 'breeding back' to some blue variety." The planting and selfing were carried out by Professor Kellerman, since Swingle had resigned before corn planting time. One

WILLETT M. HAYS
Figure 2

Professor Hays, who is to be credited with the development of the progeny test in plant breeding made many observations on inheritance of maize before 1900. His illustration of a segregating ear of maize of known ancestry was the first to be published and he approximated closely the enunciation of the principles of independent inheritance and dominance which are salient points in Mendel's discovery.

ear was obtained that had the following proportion of kernels.

Found		*Expected (our calculations)*			
deep blue	206	277	3:1	12:3:1	9:3:4
			277.5	277.5	208.1
pink	71				69.4
orange yellow	71	93	92.5	69.4	92.5
white	22			23.1	

There was one aleurone factor aside from the *Pr-pr* gene segregating. A beautiful 3:1 ratio is obtained for *Pr-pr, Y-y* or for colored-uncolored aleurone, probably the *C* or *R* factor as we know it today. Various combinations of these give an excellent 12:3:1 ratio of colored-yellow white and a good 9:3:4 ratio of blue, red, and uncolored aleurone.

The conclusions:

That the blue of the grains planted was the product of atavism, and from the fact that all the planted grains were blue, the pink, yellow and white grains in like manner must have reverted to other varieties . . . .

To show the prepotency of the blue corn, a large number of ears of other plots growing within a radius of 25 yards were examined. About half the number of unenclosed ears had from one to five blue kernels, while not one of the enclosed gave any traces of blue. This also shows the method adopted to keep out foreign pollen can be relied upon with perfect safety.

Important among the studies of early investigators who made crosses of corn was the research of Willet M. Hays of the Minnesota Experiment Station. In 1888, he made several controlled pollinations. These are illustrated by line drawings in Bulletin Number 7, of the Minnesota Experiment Station.[12] Those illustrated are five crosses, two of white sweet × yellow dent, one white dent × Crosby's Early Sweet (white), Crosby's Early Sweet × Squaw corn (flint), and a cross of white sweet × Black Mexican (sweet). Many other interesting crosses were produced. His statement concerning corn breeding is prophetic of the methods used today.

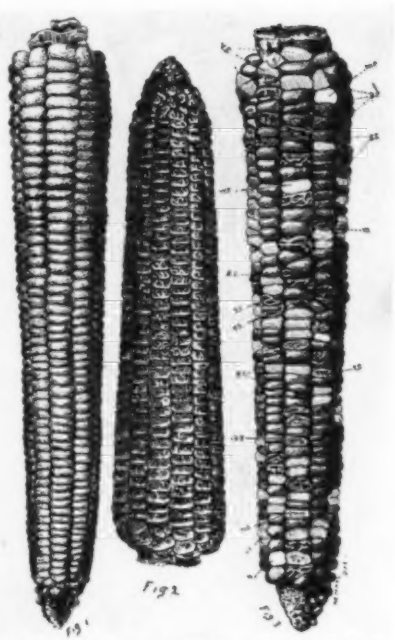
If we can so "breed" corn that the parentage on both sides can be controlled, we can more easily improve this crop by systematic crosses than any of our other field crops, on account of the great mixture of inherited qualities, making the varieties easily modified.

Hays did not have in mind producing crossed seed as is done today, but merely improving varieties by hybridization. And inbreeding as practiced today was unthought-of, as he believed corn was self sterile, that an ear could not be fertilized by pollen of the same stalk. In 1890, he published accounts of the preceding season's work.[13] When pollen of Squaw corn (flint) was applied to a white sweet ear the immediate result was reported: "—three-fourths like the male parent, resembling Flint grains, while the remaining one-fourth look like Sweet grains. There is no distinct gradation between the two kinds of grains, each one being in appearance either like

Sweet corn or like kernels of Flint; some of the latter showing only a slight tendency to wrinkle on the top." He failed to recognize that the sweet kernels were the result of pollen other than that applied although he recognized the contamination of black kernels in some of his other crosses.

The sweet and starchy kernels were planted in separate places. Hays' results are contained in the following statement: "While the Sweet grains produced ears nearly all Sweet, the kernels of Flint produced ears with about the same proportion of the two kinds as were on the parent ear produced by the cross, viz: *one-fourth Sweet and three-fourths Flint.*"* Here is a clear-cut Mendelian segregation, which was however confused with a similar ratio on the parent ear. One was the result of segregation, the other caused by poor pollination technique. Each was considered equally significant. Another interesting experiment is thus described by Hays himself.

The engraving of corn herewith, represents a very interesting case of reversion to previous more or less remote ancestors. In a field in the northeast part of the Station Farm was planted in 1888, Mercer Yellow Flint corn. Thirty rods south, across a field planted to small grains and root crops were planted a few rows of Black Mexican Sweet corn. When husking the field of Flint corn, the laborers were told to save any ears having black grains, as it was thought some of the pollen from the Black Mexican would be carried across the field, and cross-fertilize grains of the Flint. Several ears of Mercer Flint were found, each with one or a few black grains. *In no case had the Sweet variety given these grains the rough form of Sweet corn, but merely the color, while in form and hardness they resembled the Flint grains.** A dozen of these dark colored grains were planted in the vineyard in 1889, far enough away from other growing corn so that no foreign pollen reached the plants. Three or four dozen ears were produced, every one of which was a proof that the pollen from the Black Mexican corn was the male parent which had fertilized the dark colored grains on the ears of Flint the previous year. Every ear had a few or many grains exactly similar in appearance to grains of Black Mexican Sweet. These grains are shown in Figure 3, a few of which are marked B. S. The yellow Flint corn impressed its characteristics of form and color on some grains, a few of which are marked Y. F. The smooth yellow grains all have the appearance of Yellow Flint corn, and the form of the ear and cob also seemed to resemble this parent, though a few had twelve rows of grains. The Flint parent had eight rows, while the Sweet parent had, as a rule, twelve rows. Besides the Yellow Flint grains and the Black Sweet grains, above mentioned, there are Yellow Sweet, Y. S. grains, and Black Flint, B. F. grains. Even more surprising is it to find a few white Sweet grains, W. S., and a few white Flint grains, W. F., on nearly every ear. *The color of the black*



HAYS' ILLUSTRATION OF A SEGREGATING EAR OF MAIZE

Figure 3

This illustration published by Willett M. Hays in the Minnesota Experiment Station Report for 1890 is the first illustration of segregation of Mendelian characters in maize from a cross of known parentage. The ear at the right was produced on an F_1 plant of a hybrid between Yellow Flint (left) and Black Sweet (center). All of the expected recombinations of the characters involved were found on this ear by Hays but were not counted. The three center rows on the hybrid ears show 117 starchy and 31 sweet grains, a close approximation to the 3:1 ratio expected.

*Italics ours.

*Flint grains can be explained by assuming that the Flint parents form was predominant, while the color of the Sweet prevailed. And in case of the yellow Sweet grains we can assume that the form of the Sweet grains and the color of the Flint predominated.** But in the case of the white Sweet grains, no such assumptions can be made, and no better presumption appears than that the black Sweet corn had, in no distant generation, been mixed with a very light colored variety of Sweet corn; and, in case of the white Flint grains, the form is after the form of the yellow Flint parental stock, and the color may have come from a previous ancestor of white Flint, or even of white Sweet. A still further, and even stronger proof of this "breeding back," or taking the qualities of ancestors more or less remote, is the fact that on several of the ears were grains of Sweet corn showing a reddish, or flesh-colored tinge. This reddish color is peculiar to a class of Sweet corn called Early Narragansett, and the color here may be from some reversion to previous ancestors of this kind of corn, with which the Black Mexican grandparent may have been mixed.

This investigator's observations were very good. He recognized that kernels could receive the starchy character from one parent and the purple color from the other. He realized that starchy was dominant over sweet, and yellow and black over white. Thus we see that two of the tenets of Mendel's law, dominance and independent inheritance, were roughly approximated by Hays. Had he made exact counts of the ratios, he might have gone further. The corn was grown in an isolated plot so the ears were just as good as selfed ears for obtaining ratios. His material was complex, since he probably had the following factors segregating: *Su su, Y y, Pr pr,* and either *Cc, Rr* or possibly both. This would be a difficult problem, for a beginning student of genetics today. It is not surprising he did no more with it. His drawing (Figure 3), however, was accurate enough to enable a count of the sweet and starchy grains. The three most prominent rows in the drawing show 117 starchy and 31 sweet, 149 total or 20.8 per cent (approximately a 3:1 ratio).

Crozier and Rolfs[6] of the Iowa Experiment Station, Ames, Iowa, conducted some experiments to determine the immediate effect of pollen on crossed seed. Four acres of Leaming were grown along side of 15 acres of medium early white dent. In scattered places in each of these fields they planted short rows of seven different varieties. These were carefully detasseled before they shed any pollen so that all the seed produced on these seven varieties was crossed by either the Leaming or the early white. Only two varieties of sweet corn were included in these trials. One, Pride of America, crossed by Leaming, produced 8 ears, one of which was slightly shriveled like sweet. (It may have been self-pollinated.) The others resembled Canada Flint. The other cross, sweet × white dent produced 10 ears which were the same general appearance as the preceding cross. Here was definite evidence of the immediate effect of pollen, or xenia.

The second sweet corn, when crossed by the two varieties of dent corn, produced kernels resembling flint, few dented. We would expect the crossed kernels here to resemble dent more closely than flint corns, since the larger many-rowed sweet corn varieties are latent dent, while nearly all the smaller 8-rowed varieties are really flints, that have lost the ability to make normal starch grains. When sweet corn is pollinated by any starchy corn the kernels will resemble either flint or dent depending on whether they were derived from flint or dent originally.

Crozier and Rolfs used some large western dent varieties in their crossing experiment. Not all of these showed so well the effect of the foreign pollen. When white dent was pollinated by Leaming a considerable number of the ears were almost entirely yellow. The effect of xenia was probably obscured in some cases by the large, rough, deeply dented ears. The investigators set down the numbers in each case without attempting to generalize about them. Their conclusions are quite aptly stated:

In all cases some, and in some cases all, of the ears were changed in appearance in the direction of the variety furnishing the pollen. But in numbers 3 and 5 the result was nearly the same whether the pollen came from white or yellow.

They observed xenia for two characters, starchy pollen on sweet ears and yellow pollen on white ears.

(To be Concluded)

*Italics ours.

SALIVARY CHROMOSOME MAPS

With a Key to the Banding of the Chromosomes of *Drosophila Melanogaster*

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SINCE Heitz and Bauer have shown that the enormously enlarged chromosomes present in the nuclei of dipteran salivary gland cells are to be regarded as normal chromosomes rich in constant detail, and since Painter and his colleagues have demonstrated that the series of structures observable along the length of such chromosomes can be correlated to the series of genic loci on the linkage maps, it has become imperative for every Drosophila worker to make use of this new method of analysis. While the field of employment of salivary analysis is very wide, it is especially in those cases in which aberrations of the chromosomes may be involved, viz., deficiencies, duplications, translocations, inversions, etc., that the greatest saving in time and clarity of result may be expected. For such analysis two types of chromosome maps are prerequisites: first, linkage maps which give the sequence and locations of the genes for all mutant characters which may be involved, and, second, accurate detailed charts of all the normal salivary chromosomes against which to check the precise points of breakage or area of disturbance. A necessary adjunct to the detailed maps of the chromosome banding is an objective system of referring to a particular band or section of a chromosome. The general adoption of a system of "Salivary chromosome coordinates" by workers in this field is thus a matter of prime importance. The plan outlined below has proved in practice to have great advantages in being both accurate and elastic.

For many years I have maintained current linkage maps summarizing the genetic evidence on the locations of genes. These have been published from time to time, and revised copies have also been sent to many individuals upon request. The latest revision will appear in a forthcoming number of this JOURNAL and will be distributed widely through the "Drosophila Information Service."

The Wealth of Detail Observable in Salivary Chromosomes

Painter has just published in this JOURNAL (December, 1934, pp. 465-476) his survey of the normal salivary chromosomes, with maps which show the salient features. But, as he states, the amount of detail to be seen in the chromosomes is far in excess of that shown. During the past year I have attempted to make, for the structures of the normal salivary chromosomes, maps which would show this finer detail. Such detailed maps were found indispensable in precise study of chromosome aberration. They are herewith presented at a magnification sufficient to carry most of the detail, though to insure that the faintest lines observable be not lost entirely in reproduction, it has been necessary to sacrifice much of the range of intensities in the original drawings which were shown at the annual exhibit of the Carnegie Institution of Washington, December 14-17, 1934. Hence in using these maps it must be remembered that the fainter lines of the chromosomes and the fainter areas appear disproportionately too conspicuous and dark upon the maps reproduced herewith.

Refinements Which Aid Observation

For observing the finest detail several refinements of technique are required.

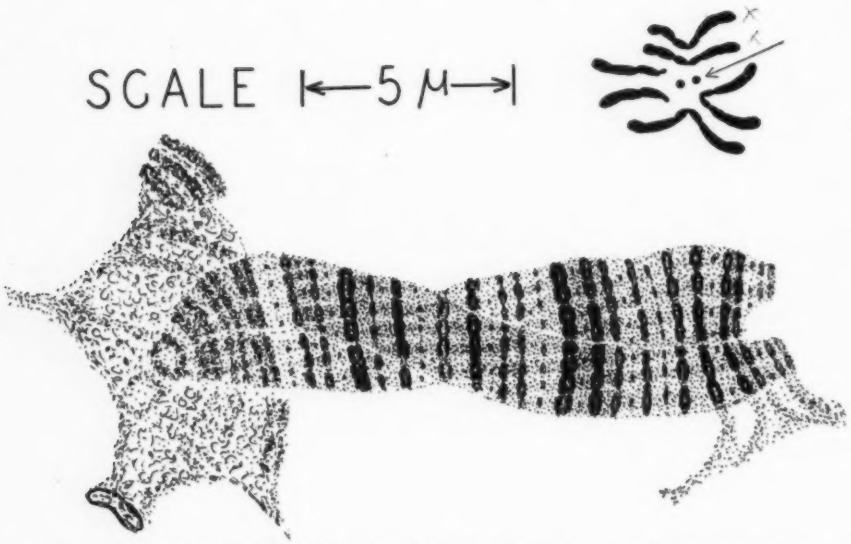
One is relatively light transparent staining of the chromosomes, with avoidance of heavy "contrasty" staining, which may give the heavy lines very dark but the lighter lines not at all. Much iron and heating tend to spoil the finer details. The crispness of detail seen in larvae fully grown in pair cultures at a low temperature is lost in larvae from old cultures, from mass cultures and in larvae which have begun pupation. Especially favorable material has been attached-X (*XXY*) females of the race giant bobbed-11 picking giant larvae and examining the double-thickness chromosomes of certain cells found there.

Another requisite is selection of chromosomes or portions which are straight (i. e., not kinked or coiled) and are stretched somewhat. The lax chromosomes are from 70 to 110 times as long as normal gonial chromosomes, but the somewhat stretched chromosomes which are most favorable for observation are 150-160 times normal length. The maps presented herewith are drawn only from such partially stretched chromosomes, averaging 150 times normal. (For comparison a gonial group at the same magnification is included.) The gross structure of salivary chromosomes is somewhat like that of an accordian, and unless these chromosomes are stretched the doubleness of most bands is not visible and many fine or dotted lines are obscured by their appressed neighbors.

Too much attention cannot be paid to the illumination of the chromosomes. I use a 6-volt ribbon-filament lamp, and control intensity by a 175-ohm 2 amp. variable resistance in the 110-volt current to the transformer. The light from the ribbon is brought to a sharp focus in a small-area image about 30 cm from the filament and 25 cm from the mirror. This image is diaphragmed at that point to a circle the width of the ribbon image (3.5 mm). For turning the red color of the stain black, I set up Wratten filter 58A (deep yellowish green) behind one or more cobalt- blue glasses just before the mirror. A front-silvered or aluminized mirror is preferable. An achromatic 1.3 or 1.4 condenser, oil-immersed, should be focused so that the edge of the filament image and/or the edge of the diaphram are sharp in the field observed. The substage diaphragm should then be gradually closed down, with compensating adjustment of light intensity by the rheostat, until the area outside the image of the filament loses its light-haze and becomes dark, while the details of the chromosome banding increase in sharpness and contrast. Final checking should be made by oblique light (decentering the substage diaphragm) cast along the axis of the chromosome. I prefer 120× apochromatic objective with 10× compensating ocular for observations, but a 90× with 10× or 12.5× eyepieces does nearly as well and does not require such critical attention to illumination, cover glass thickness and other details.

A System of Cataloguing Salivary Bands

The system of chromosome map nomenclature proposed in this paper divides the five main chromosome limbs (1=X, 2L, 2R, 3L and 3R) each into twenty sections, 100 in all. Sections are numbered 1 to 20 for X, 21 to 40 for 2L, 41 to 60 for 2R, 61 to 80 for 3L and 81 to 100 for 3R. Chromosome 4 has sections 101 and 102. Hence the number of a section is itself a key to the chromosome limb and to the relative position along that limb. Since sharpness and definiteness are essentials, each section begins with a conspicuous and easily recognized band. The division point is always made just to the left of the chosen main band, leaving all minor bands inside the division to the left of it. But since the 102 divisions average over 25 bands each, six subdivisions have been established for each division. Each subdivision also begins with a sharp band. They are designated by the capital letters A to F. A particular band would then be referred to as 17B3; a break would be referred to as just to the left



SALIVARY CHROMOSOMES AND GONIAL CHROMOSOMES COMPARED

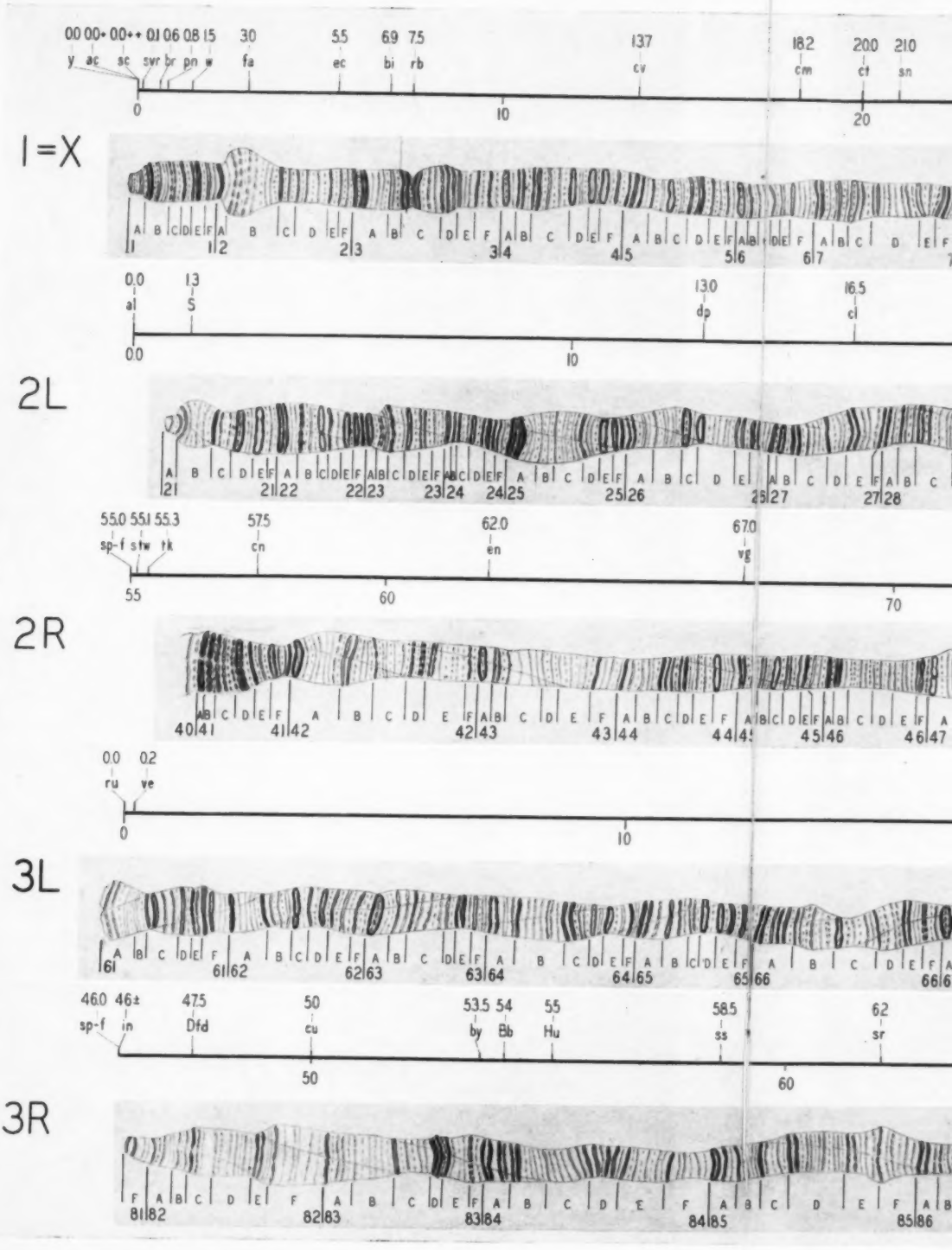
Figure 4

Drawings of chromosome 4 of *D. melanogaster* and, on the same scale, of the entire group of gonial chromosomes at metaphase. In this gonial group the paired fourth chromosomes are represented by the small black dots, in which no structural details can be seen under the highest magnification, in striking contrast to the wealth of detail visible in the salivary chromosomes.

of 42C2 and a section as extending from 36A1 (included) to 38B1 (not included). The bands are not given definitive numbers on the maps because those numbers would change from year to year as our knowledge of the banding becomes more detailed and small bands are seen which were previously missed. No such change should be necessary for the divisions and subdivisions, since each begins with a sharp band already well established.

Landmarks of the Chromosomes

The "segmentations" observable in the chromosomes do not offer sharp enough boundaries for a serviceable reference system, though certain ones are very convenient landmarks for recognizing chromosomes in a tangle. Among the natural landmarks which should be learned first are the "puff" in 2B, the "four brothers" in 9A, the "weak spot" in 11A, the two "chains" in 15, the "turnip" in 16 and the "offset" in 19E. The huge lightly staining nucleolus of the salivary gland cell nucleus is attached to the base of the X at the bands in 20C and D. Diagnostic of 2L are the "dog-collar" in 21CD, the "shoe-buckle" of 25A, the "shield" in 30A, the "goose-neck" in 31BF, the "spiral loop" of 32-35, a "turn-back" in 36, and the "basal loop" in 37-39. One recognizes 2R by its thick "onion" base and "huckleberry" tip. Three L has a "barrel" at 61CF, a "ballet skirt" in 68BC, "chinese lanterns" in 74-75 and "graded capsules" in 79CDE. Finally, 3R, the longest limb, has a large clear "cucumber" base 81-83D, a "duck's head" at 89E to 91A (frequently breaks at junction of 89D and E) and a "goblet" tip. Most of the apparent segmentation is inconstant and is due to the fact that the maternal and paternal part-


0.0 0.0+ 0.0++ 0.1 0.6 0.8 1.5 3.0 5.5 6.9 7.5 13.7 18.2 20.0 21.0
y ac sc svr br pn w fa ec bi rb cv cm ct sn
0 10 20
1=X
A B C D E F A B C D E F A B C D E F A B C D E F A B C D E F A B C D E F A B C D E F A B C D E F A B C D E F
1 1|2 2|3 3|4 4|5 5|6 6|7
0.0 1.3 13.0 16.5
al S dp cl
0.0 10
2L
A B C D E F A B C D E F A B C D E F A B C D E F A B C D E F A B C D E F A B C D E F A B C D E F A B C D E F A B C
21 21|22 22|23 23|24 24|25 25|26 26|27 27|28
55.0 55.1 55.3 57.5 62.0 67.0
sp-f stw tk cn en vg
55 60 70
2R
A B C D E F A B C D E F A B C D E F A B C D E F A B C D E F A B C D E F A B C D E F A B C D E F A B C D E F A
40 40|41 41|42 42|43 43|44 44|45 45|46 46|47
0.0 0.2
ru ve
0 10
3L
A B C D E F A B C D E F A B C D E F A B C D E F A B C D E F A B C D E F A B C D E F A B C D E F A B C D E F A
61 61|62 62|63 63|64 64|65 65|66 66|6
46.0 46± 47.5 50 53.5 54 55 58.5 62
sp-f in Dfd cu by Bb Hu ss sr
50 60
3R
F A B C D E F A B C D E F A B C D E F A B C D E F A B C D E F A B C D E F A B C D E F A B C D E F A B C D E F A B
81 81|82 82|83 83|84 84|85 85|86

Supplement to *Journal of Heredity*, Vol. 26, No. 2, February, 1935 (To follow Page 62).
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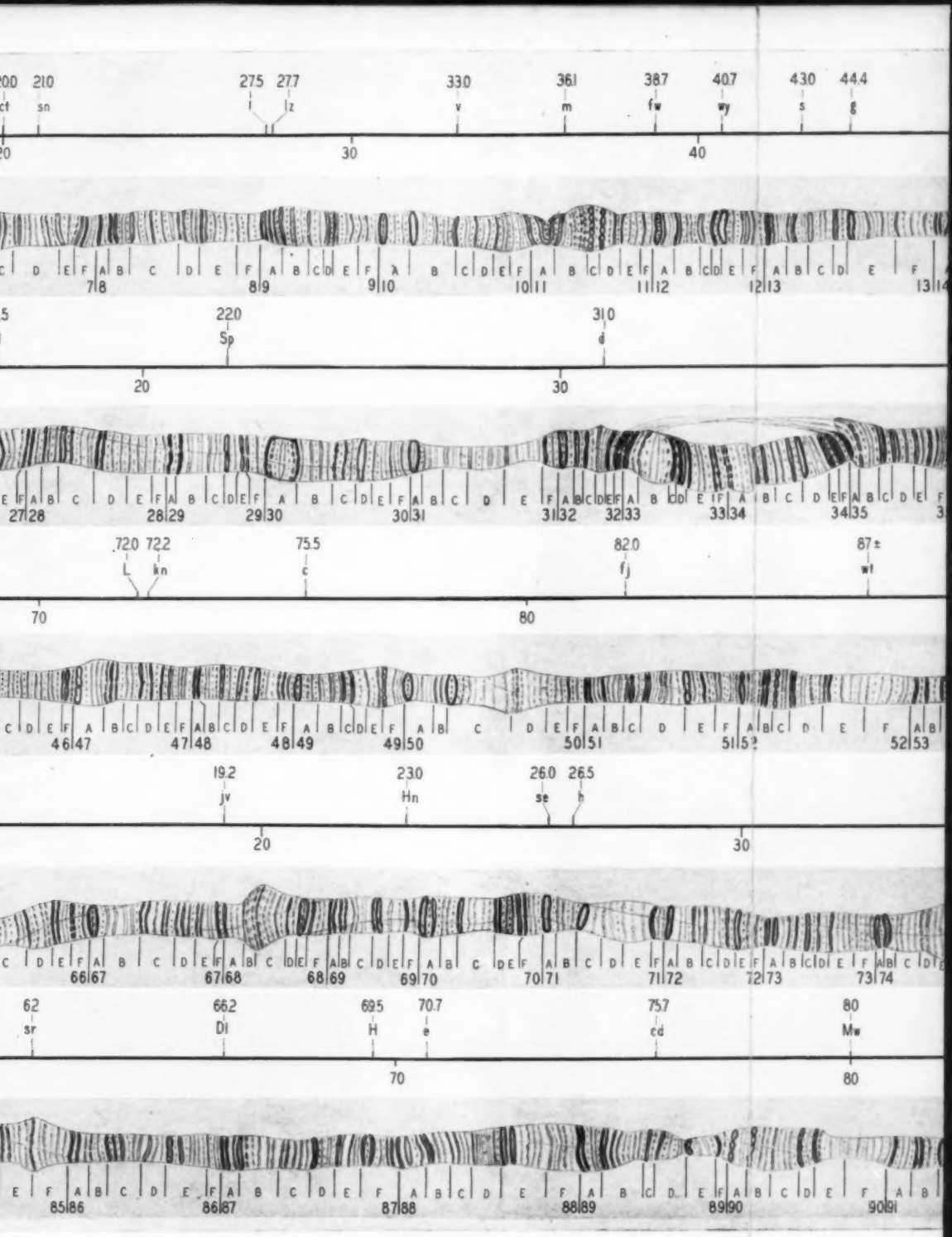
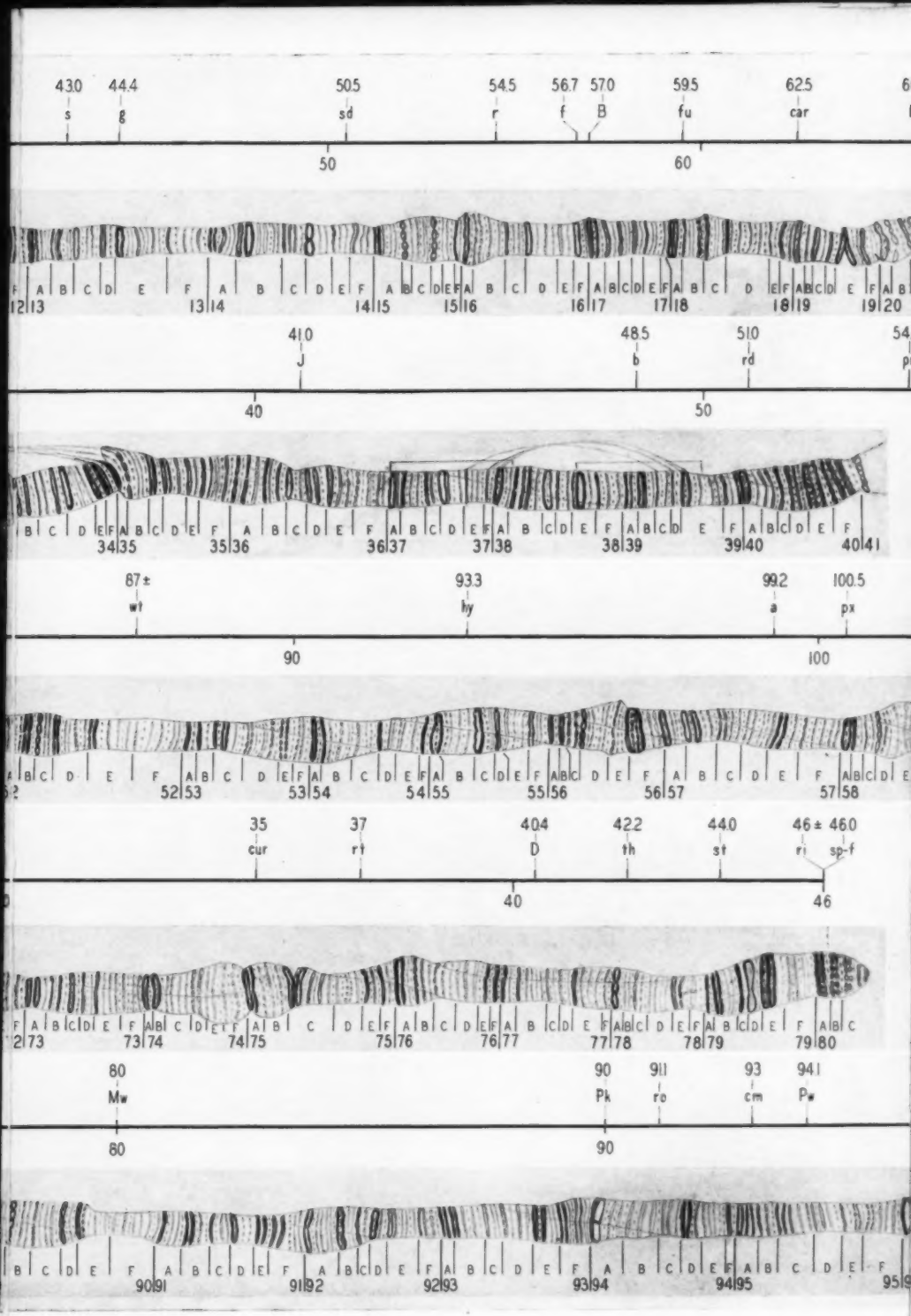


REFERENCE MAP OF THE SALIVARY CHROMOSOMES OF DROSOPH

Figure 5



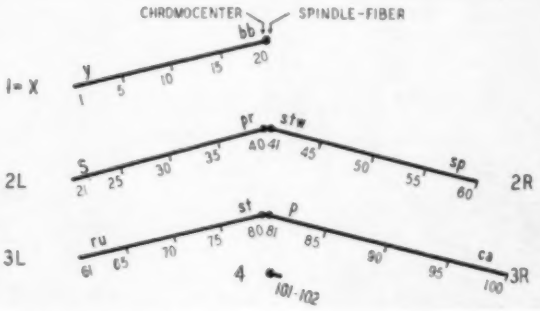
SOMES OF DROSOPHILA MELANOGASTER

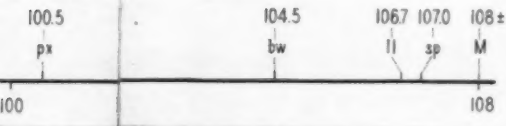
5

KEY TO REFERENCE SYSTEM FOR SALIVARY CHROMOSOMES

DIVISIONS, NUMBERED IN GROUPS OF 20 (1-102)
Each begins with a major band

SUBDIVISIONS, LETTERED IN GROUPS OF 6 (A-F)
Each begins with a sharp band



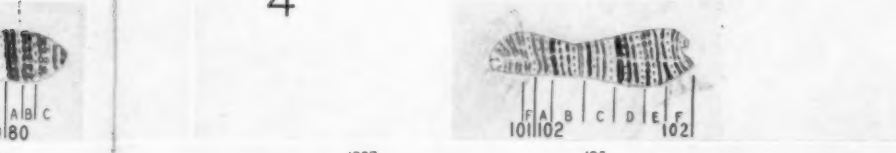


SCALE ⊢—10μ—⊣

CHROMOSOMES OF NORMAL FEMALE

GONIAL CELL

4



ners are sometimes seen side by side, as in section 25, and sometimes superimposed, as in section 24.

The free end of every chromosome limb presents a characteristically narrowed terminal region, seen especially clearly in the maps at 1A, 21A, 60F, but present also in part in 61A, 100F and 102F. It is suggested that this narrowed region represents a lag of one division in the gene-strings, somehow due to the terminal position occupied but not due to special properties of those particular genes.

Size and Structure of the Chromosomes

The average lengths of the moderately stretched salivary chromosomes as drawn are: 1 = X = 220 μ; 2 = 215 + 245 = 460 μ; 3 = 210 + 275 = 485 μ; 4 = 15 μ; total = 1,180 μ. Thus the total length of the moderately stretched salivary chromosomes is approximately 150 times that of the total length of the gonial chromosomes, which is 7.5 μ. Individual salivary chromosomes with lengths exceeding 180 times normal have been measured. These excessively stretched chromosomes or portions show most of the stretching in the hyaline zones between the dark "bands." The heavier cross-bands or capsules retain their shape as broad firm discs while the material between may stretch into a narrow cord ten times its normal length but still showing its compound nature.

As deduced independently by Dr. Koltzoff (*Science*, Oct. 5, 1934) and myself (in press in U. S. S. R. since June, 1934) the large size of the salivary chromosomes is partly due to their being compound structures. Each of the fused maternal and paternal homologues consists of eight chromonemata or gene-strings derived from the corresponding chromosome of the gamete by successive divisions without complete separation of the division products. The cable of 8 + 8 strands shows its structure most clearly in the less heavy cross-bands in which 16 individual dots, vesicles or small capsular units may be seen.

The Relation of the Genes to the Bands

My inference as to the relation of the genes to the structures seen in the salivary chromosomes is that each of the faint cross-bands made up of 8 + 8 dots (see last line of 102D), dashes (middle line of 102E) or vesicles (first line of 102E) corresponds to one locus with 8 maternal and 8 paternal sister genes. I suppose that each of the sister genes of a locus is enclosed within one of the vesicular units, the gene itself being small and unstained but the walls of the enclosing capsular or clam-shell structure being visible from a deposit of chromatin. If the bipolar deposits of chromatin are somewhat heavier they run together at their edges to form two thin discs, one on each side of the plane of the genes. This hypothesis is in line with the observation of large numbers of thin bands (like those in 102A) which in edge view are wavy close doublets like the two halves of a split pea-pod. With still heavier deposits of chromatin, in amount characteristic for each locus, heavy obscurely double and somewhat nodulated bands result (like the first in 102B).

But besides these "thin-walled" structures there are "heavy-walled" structures (such as the first in 4F) which seem better interpreted as compound bands made up of two bands more or less united at their edges to give a "heavy-walled capsule." In very good preparations some of these heavy-walled capsules can be seen as two parallel bands not united at their edges. Certain of the heavy-walled capsules would seem to correspond to three loci, since they enclose between them a line of dots or dashes (4A1; 6A1; 7C1, etc.).

A count of the distinctly seen "lines" in the salivary chromosomes gave approximately 725 for X, 1,320 for 2, 1,450 for 3 and 45 for 4, totaling 3,540 lines. But a considerable proportion of the above lines seem incipiently double

or with an indistinct split. A count of "bands" or "loci," on the basis that each line of dots, dashes or vesicles and also each pair of closely approximated thin or moderately heavy lines represents one locus, while each heavy-walled capsule represents two (or three) loci, yielded: for X, 537; for 2, 1,032; for 3, 1,047, and for 4, 34 "bands." The total of 2,650 bands is in good agreement with calculations of 1,500 to 3,000 genes for the animal.

Direct and Reversed Repetitions of Series of Bands

A structural feature of the highest theoretical importance is shown clearly in the "loops" and the "turn-back" in the basal half of 2L. Great difficulty was encountered at first in studying the base of 2L because of the troublesome kinks and coils. But in some cells the spiral coils were found stretched nearly straight and then it was observed that the edges of certain bands had been fused together and had been stretched out into connecting threads. The connected bands were found to match morphologically, 32F to 33C with 34F to 35C, in a whole series of repeated bands. The spiral loop was due to synapsis between homologous series of bands in two different positions in the same chromosome. Similarly, the basal loop in 37 and 38-39, when stretched out, revealed connecting strands linking (for example) the bands in 37EF and 38A with bands of identical morphology in 39CDE. Further study showed that all the bands in 37 were at least roughly matched in 38E to 39E (bracketed).

The "turn-back" in 36 with side by side fusion and the "shield" in 30A show reversed series forming sections symmetrical about their center points. It is significant that the bands in 30A show fusion along the surface of the chromosome to give a giant capsule. This suggests that most of the larger capsules, such as the four-banded ones in 25A and in 56F, are symmetrical reversed repeats. The reversed symmetries around "weak spots" 3C and 11A may be further examples of duplications of sections of homologous bands.

How complicated a structure could be built by successive direct and reversed repeats is perhaps illustrated by the reversed symmetry with capsule tendency which centers around 33B and which is itself a part of the series repeated in direct sequence in 34-35.

The thick-walled capsules like that in 21E, some of which seem to enclose a line between them, as in 21D, may represent single-band or short repeats. There are also large numbers of pairs of lines of equal intensity, like that in 27E, the members of which are definitely separate. Perhaps some local process, such as unequal crossing-over, may have to be invoked to account for them.

The Role of Duplications in the Evolution of Chromosomes and the Initiation of Species

For the long repeats, both direct and reversed, an origination as duplications through the process of translocation would seem an adequate explanation. In my first report on duplications at the 1918 meeting of the A. A. A. S., I emphasized the point that the main interest in duplications lay in their offering a method for evolutionary increase in lengths of chromosomes with identical genes which could subsequently mutate separately and diversify their effects. The present demonstration that certain sections of normal chromosomes have actually been built up in blocks through such "repeats" goes far toward explaining species initiation. For the duplication of sections of genes is known in Drosophila to cause many slight poorly-defined differences in all parts of the duplicant type.

AN EARLIER RECORD OF THE TOOTHLESS MEN OF SIND

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In Thadani's recent addition[4] to his former note[3] on sex-linked anadontia associated with anhidrosis in the "Bhudas" of Sind, he states that "no records, either written or from memory are available about the first two generations." Since the following sentences from Darwin[1] have apparently not been noticed by Thadani or by Gates, Popenoe, Castle, Roberts and others who have cited his first report in their writings on heredity in man, their repetition here seems justified.

> . . . . I may give an analogous case, communicated to me by Mr. W. Wedderburn, of a Hindoo family in Scinde, in which ten men, in the course of four generations, were furnished, in both jaws taken together, with only four small and weak incisor teeth and with eight posterior molars. The men thus affected have very little hair on the body, and become bald early in life. They also suffer much during hot weather from excessive dryness of the skin. It is remarkable that no instance has occurred of a daughter being thus affected; and this fact reminds us how much more liable men are in England to become bald than women. Though the daughters in the above family are never affected, they transmit the tendency to their sons; and no case has occurred of a son transmitting it to his sons. The affection thus appears only in alternate generations, or after long intervals . . . .

The syndrome reported by Darwin's correspondent is obviously identical with that described by Thadani. Since both accounts come from the province of Sind in north-west India, it is reasonably certain that the Darwinian quotation refers to the earlier generations of the family reported by Thadani (The Sind of today and the Scinde of Darwin's day are identical.) Darwin's account is given in the second edition of "Animals and Plants," which appeared in 1875, but not in the first edition of the same work, published in 1868. This suggests that his correspondent wrote between these two dates. Assuming that in this country there would be a span of approximately twenty years between generations, it would appear that Mr. Wedderburn's four generations cover the period from about 1780 to 1860 (since he refers to "men" and does not mention any children), while Thadani's four generations probably extend from about 1850 to 1930.

The data, incomplete though they be, apparently include from six to eight generations. One wonders if Darwin's correspondent gave any more details than are found in the quotation above. Possibly a search through Darwiniana at Down House, Burlington House, the British Museum and elsewhere might bring Mr. Wedderburn's letter to light. Should it permit the formation of a pedigree chart covering these earlier generations, it should not be difficult to fit the earlier history to the later one, and, with some amplification of Thadani's data, it might be possible to construct a pedigree chart covering seven or more generations of this interesting sex-linked character.

The fact that four affected females occurred in Thadani's later generations, while none were known to Darwin's correspondent, suggests that in this pedigree, as in those of some other sex-linked characters, there have arisen aberrations in the mechanism of inheritance, or in the behavior of the gene. However, among five generations of an American family exhibiting exactly the same syndrome, Roberts[2] found five partially affected females, some of whom showed no more evidence of it than occasional patches of skin lacking sweat glands. Such a partial manifestation might have been entirely missed by Darwin's informant. It seems more likely, therefore, that in the Indian family the

exceptions to the conventional behavior for recessive sex-linked characters occur because the gene is not completely recessive in heterozygotes (which are always females). Such a condition is not to be unexpected for a gene having such profound effects in hemizygous (*XY*) persons.

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3. Thadani, K. I., 1921. A toothless type of man. *Journ. Hered.*, 12: 87-88.
4. ————, 1934. The toothless man of Sind. *Journ. Hered.*, 25: 483-484.

The Brahma-Plymouth Rock Mosaic

I HAVE been much interested by the description and pictures of a Brahma-Plymouth Rock mosaic fowl published in the Journal of Heredity for January, 1935, by Roberts and Quisenberry. The case is quite without parallel among previously described examples of mosaic birds or mammals, in that it involves, simultaneously, genes located in more than one chromosome and at the same time mosaicism of general body size. It seems to me that none of the explanations suggested by the authors can adequately account for the production of this remarkable bird, although an adequate explanation is hinted at by them in the remark that "the father, if only one is involved," was "probably a Brahma."

If there were *two* fathers, instead of one, one being a Brahma, the other a Plymouth Rock, the observed characteristics of the mosaic bird would naturally result. The mother, beyond question, was a Plymouth Rock. A sperm from a Plymouth Rock male, fertilizing the egg, would produce the kind of structures found in the right half of the mosaic bird,—viz., (1) barred feathers, (2) clean leg, (3) medium size of body. A sperm from a Brahma male, fertilizing the egg, would produce the structures found in the left half of the mosaic,—viz., (1) Brahma (Columbian) plumage pattern, (2) feathered leg, (3) larger body size.

But could an egg be doubly fertilized and yet produce a single embryo? No previously described case among birds or mammals is known to the writer, but among insects such an occurrence has been fully established. Goldschmidt and Katsuki* have shown that in a certain strain of silkworms a double fertilization of the egg frequently occurs, resulting in the production in successive generations of individuals which are lateral mosaics as regards sex or as regards other characters for which the mothers were heterozygous. A cytological study of the case showed that two haploid egg nuclei were in such cases fertilized, each by a different sperm, the egg nuclei corresponding probably with the ordinary egg nucleus and the second polar nucleus respectively.

Similarly, in the case of the fowl, we have only to suppose that two egg nuclei capable of fertilization were in some way produced, that a Plymouth Rock sperm united with one, a Brahma sperm with the other. From the embryonic tissue thus produced a single embryo resulted.

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Biol. Zentrbl. 51: 58-74. 1931.

SIX VIEWS OF MAN

New Books on Various Phases of Human Biology Consider a Wide Variety of Problems

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STUDIES IN HUMAN ECOLOGY

THIS addle-pated world makes some queer distinctions. One finds them even in science. Take biology, for example. In ordinary work among lowly organisms, it is thought desirable to select simple problems, capable of exact statement, direct attack, and concrete solution. Hence the ecologist is held in slight esteem as a young and imprudent brother who has a perpetual headache from trying to do too much. In human biology, however, the situation is different. Here the anatomists, the physiologists, and the physicians are rated as simple-minded plodders low in social value; while the ecologists—calling themselves economists and sociologists, yet being merely expositors of the mutual relationships between man and his environment—are set on high and give council to the great.

This inverted state of affairs found in human biology is fraught with grave consequences; for these Jupiters of economics and sociology have no laboratories filled with guinea pigs upon which to try out the theories which spring, Minerva-like, from their fertile brains. Consequently, they yearn to put their schemes, into general operation; and owing to the sad after-effects of the late war, such desires are encouraged, with unusually dire results.

Since something should be done about the matter, the present writer suggests that a change in educational policy be made requiring, as a sort of birth control measure, that all fledgling human ecologists study the Population Problem for ten full years before being allowed to practice. After this experience, all their vigor will have been sapped away, and their theories, if they have any, will disturb nothing but the leisure of reviewers.

But perhaps this suggestion is unnecessary. The plan may already be in operation; for the same mail that brought for comment the population studies of Lorimer and Osborn* and of Penrose,† brought also the third number of *Population*, the official journal of the International Union for the Scientific Investigation of Population Problems, published under the editorship of E. C. Rhodes of the London School of Economics. In this issue, besides eight articles in three languages, there were reviews of three population books and advertisements of nine others.

Of the two works in hand, that of Lorimer and Osborn appears to hold more substantial and lasting values. It is not entertaining; it offers no novel ideas; it advances no revolutionary theories; it produces no unsuspected conclusions. Nevertheless, it has great merit as a storehouse of demographic material relating to the United States, all carefully gathered and soberly evaluated. In this labor, which must have been enormous, the authors had the aid of a greater galaxy of specialists than are usually enlisted in an effort of this kind.

The material is treated under four headings, each comprising several chapters. In Population Trends, an analysis

*Lorimer, Frank, and Frederick Osborn, *The Dynamics of Population*. Pages, XIII, 460. Price, $4.00. The Macmillan Company, New York, 1934.

†Penrose, E. F., Population Theories and Their Application with Special Reference to Japan. Pages, XIV+347.

is made both of the growth of the United States as a whole and of communities of various sizes. There is also an extended consideration of the reproductive tendencies of peoples having different origins and belonging to different occupational groups. In Measurable Characteristics of American Groups, the authors have examined health, culture, and intellectual background. In Influence of Differential Reproduction, the significance both of biological and of social differentials is explored. In Causes and Control of Population Trends, there is a careful scrutiny of the physical, economic, and social factors influencing fertility, which serves as a background for observations on the possibilities of conscious adjustment through changed conditions. A series of twenty-three appendices presenting special data, a glossary, an extensive bibliography, and a very satisfactory index comprise the remainder of the volume.

One gathers that Lorimer and Osborn had in mind the production of a dependable compendium of facts concerning the population of this country without having them trammeled by extraneous theory. If so, they did a good job; and this leaves little for a reviewer to say. Yet it seems worth while to repeat here a few of the conclusions obtained. Their importance is not lessened by their lack of novelty.

The United States is tending rapidly toward a stationary population. During this process fertility differentials are disappearing as between negroes and whites and as among peoples of different national origins, though an advantage is still retained by the women of certain minor groups, among which may be mentioned Mexicans, Chinese, Japanese, Amerinds, and French Canadians. The most notable fertility differential, and one which will probably persist over a period of years, is that held by the rural districts over the urban districts. One of the most vexing questions with which the next generation must deal, therefore, is how to adjust economically to a population that will have much higher proportionate numbers in the higher age-groups, and how to provide opportunities for the lads and lassies who form excessive replacements on the farms where, owing to increased mechanization, smaller and still smaller numbers are required. According to the authors, "the most serious economic aspect of present population trends in the United States is the accumulation of surplus population in agricultural areas with limited natural resources." A somewhat comparable problem is presented by the increase shown in the families of unskilled laborers during a period when demand is diminishing.

The studies of variations in hereditary differences in intellectual capacity yielded negligible results except when based on occupational status, a result similar to that found by Havelock Ellis years ago. Though there is overlapping, indicating a reservoir of individuals in the lower social groups having a capacity to rise, the available evidence suggests that the negative correlation between fertility and social status "involves a gradual decline in average capacity for intellectual development." Such a trend, if continued, would necessarily result in lowering the American cultural level. In contradistinction to this result, the authors do not find dependable data from which to check the often maintained thesis that there is a difference in the average level of intelligence exhibited by populations of unlike racial origin. There was even less evidence of intellectual differences among large regional groups, or between farm people and city people; and the same statement may be made as to differences in indicated physical vigor. There was, however, significant evidence that those having lower cultural resources were out-peopling those having higher resources.

The dangers inherent in these last findings are considered in some detail by the authors in the chapter on social control. The suggestions made include the improvement of conditions both in rural communities and in the cities, further restriction of immigration, greater economic security for the young, adequate and proper contraceptive advice,

and voluntary sterilization. There is a tendency here to avoid the use of the word *eugenics*, though the measures involved are all eugenical in import, and the problems as set forth are largely those of eugenics as defined by Galton. If this fact be recognized, the alternative solutions are birth release by the more highly endowed or birth restriction by the intellectually handicapped. Lorimer and Osborn appear to favor the former, though why this should be the case is questionable, in view of the superior numbers of the handicapped, especially when the paternalistic measures of our present government are fast breaking down the self-reliance and ambition of this group.

Japanese Population Problems

The Penrose work is much more interesting than the one just described, but is inherently less valuable. This is not because it has special reference to Japan rather than to the United States, but because the author presents a rather limited amount of data to substantiate his views and because he is a victim of that distressing habit common to many economists of using a microtome on every theoretical hair. For example, there are forty-six pages devoted to the precise meaning of Malthus in his famous Essay and whether or not he was consistent in his conclusions. All of which has been done many times before and done better. The criticism of the income optimum theory of population, however, is clear; and the exposition of the welfare optimum theory has many points of excellence.

When the author leaves theory and writes of the concrete aspects of the Japanese Population Problem, there is real substance in what he has to say. It should also be noted that this portion of the essay is as well documented as is possible with a phase of the subject where acceptable data are meagre. It is the opinion of most western writers that the Japanese are a very fecund people, living in a comparatively barren country that is even now over-populated; and Japanese writers themselves have made similar statements in explaining recent events in Manchuria. Penrose, however, believes that there is no support for the view that the Japanese are extraordinarily fertile. He finds that the highest recorded birth rate is less than 35 per thousand (date not given), and concludes that the increase in the Japanese population has been attained by birth rates and death rates wholly comparable with those of Europe. Furthermore, he believes that for the past decade or longer, the birth rate has been falling rapidly, owing to the increased use of contraceptive measures. It is therefore probable, and in this he is following Uyeda, that the annual number of births during the next twenty years will remain close to 2,100,000, and that the death rate will remain stationary. If this expectancy is attained, stability in the group of reproductive age will be reached by 1950 and will drop thereafter. Thus the ultimate population of Japan will be somewhere between 80,000,000 and 100,000,000.

The food for this population apparently can be produced as far as quantity is concerned; the grave deficiencies are qualitative,—a lack of proteins and vitamins. Nevertheless, the per capita income has been rising since the beginning of the twentieth century, owing to increased industrialization; and with this growth there is indication that the food habits are changing for the better. The author believes that the industrialization thus begun will continue over a considerable period of time, and that Japan will be faced with shifting rural people to the cities just as has the United States. Doubtless this conclusion is correct in face of no definite predictions as to the magnitude of Japan's industrialization. But the author's apparent conviction that this social change will be less limited by a dearth of natural resources and a lack of originality in invention than most western writers believe, is not convincing.

The remaining portion of Dr. Penrose's work, and the longest section, is taken up with an examination of the bearing of population upon migration,

territorial expansion, and international trade. In these considerations, the author expresses opinions freely and, though not didactic, tends to favor the view that the rights of people in over-populated lands to spread their nationals abroad are paramount to the rights of people in under-populated lands to control the territory now under their jurisdiction. Here there is a significant failure to treat the effects of admixtures of different social customs on the situation. Other specific criticisms might be made, were space available. They can be summed up, however, in the general statement that the author often fails to distinguish essentials from non-essentials. Others, however, may not feel that such criticisms are sound; therefore the reviewer feels that every student interested in the subject of population would do well to mill the book and sift his own wheat.

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EUGENICS TODAY

THIS is a revision after fifteen years, of one of the first books on the application of eugenic methods, which has come to be used as a college textbook.* The changes in the world in political and economic and industrial life during the intervening period have been accompanied by a great increase of research in many countries into the forces of heredity and environment and the possibility of applying eugenic reform as a means of helping the world to a better and happier condition.

The book gives an account of the results of this work along many lines of enquiry. A great deal of fresh information is thus added, based on the enquiries of the last decade, which does not involve, at the same time, any change in the social philosophy or the technology of eugenics.

Abundant references are given at the end to all original investigations quoted in the text, so that the book serves for reference for the student, as well as for a more popular work for those interested in questions of social and especially eugenic reform.

Problems of race, and of social reform, of the structure of modern society, and social legislation and education are all introduced in their bearing on eugenics, and a summary is given of the recent attempts of different governments to apply eugenics in their programs of social reform. The cases of the United States of America, the Soviet Union, and other European countries, as well as China and Japan, are quoted especially in this connection.

The writer emphasizes the point that the cause of eugenics must also be promoted by encouraging larger families of the fit as well as by the elimination of the stocks of the unfit.

There is a particularly interesting and helpful appendix giving problems for the use of students. In formulating answers to these questions students are encouraged to notice the working of heredity in daily life among their relatives and friends and associates, and in its bearing on their own character. They also emphasize the need of viewing all the problems of eugenics from all standpoints.

An elementary knowledge of statistics is assumed, and the student who makes use of this scheme of self-teaching must surely be led to a great deal of research work. These questions assume that the enquirer is able fairly easily to obtain reliable information as to, for example, the family

*Popenoe, Paul, and R. H. Johnson. *Applied Eugenics.* The Macmillan Company, New York, 1933.

history of a mental defective, or personal information about the people round him. This, in practice, is found to be one of the greatest difficulties, since people are often reluctant to give information even to one who is authorized to make enquiries.

The small amount of information obtained in this way cannot perhaps be of much value, but will lead the student to appreciate the need of abundant statistics, and to learn the modern methods of statistics for the analysis and reduction of data, which must be the basis of all knowledge of heredity applied to human society.

The questions show the wide scope of the science of eugenics, involving, as it does, not only biology and statistics, anthropology, and social reform, but also religion, psychology, and education.

The need is shown in this book of an appreciation of the different kinds of selective factors at work in human society; and some research into official records is encouraged.

The research required for the questions dealt with in this book will reveal the difficulties of the practical problems of eugenics, and the possibility of the best intentioned efforts of social welfare agencies being dysgenic in effect. It will also serve to stimulate an interest in the social and charitable administration of the community.

The book must thus serve as a most useful guide to all the many questions relating to the application of eugenics.

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NATURE AND NURTURE IN MENTAL DEVELOPMENT

A DIAGRAM on page 173 of this book* shows the numbers of the "more significant research contributions" to the study of the "heredity-environment" problem which were published each year between 1905 and 1932, and the decline since can be attributed to economic conditions rather than to any loss of interest in the subject. It requires a large volume such as this one to summarize and coordinate the useful research work which has been carried out with the object of assessing the relative influences of nature and nurture in determining the psychological characteristics of the individual, and it is obviously impossible to summarize such a summary in a short notice of it. The problem can be approached from several different angles and there are pitfalls in every road. The author has limited her survey in one direction by gathering most of the data discussed from studies which have appeared in the last decade, and several which a future generation may value more highly seem to have been neglected in this way. A certain bias is shown, too, in that American publications are considered more than European. But it is clear that this book provides a conscientiously prepared critical résumé of a great deal of the best work which has been carried out in all countries, and it should prove a valuable guide to all psychologists and eugenists. The impetus to modern research in this field was given, as the author fully recognizes, by the discovery that mental traits are capable of being measured—though what particular character is measured by a particular test is often a matter of conjecture—and by the

*Schwesinger, Gladys C., *Heredity and Environment.* Edited by Frederick Osborn. The Macmillan Company, New York, 1933.

simultaneous growth of methods of statistical analysis which made possible an adequate treatment of the new data. The historian may have no doubts concerning a particular event as long as only one document bearing on it is known, but the discovery of other documents can embarrass him: in scientific matters, too, it often happens that additional evidence does not clarify a particular question at once. The new technique which is being used to examine the question of nature and nurture has already revealed the complexity of the problem, and there is every hope that it will ultimately lead to a satisfactory solution. This book is a useful guide to what has already been accomplished and to what remains to be done.

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GENES AND THE UNCONSCIOUS

THIS volume* is an interesting account of the growth of psychiatry in the United States during the past 40 years. It recounts the transformation from the old system where as little was done for the patient as possible, to the present system where everything is done for the patient; it records the development of the social attitude which resulted in the "insane" being changed into the "mentally ill."

It is not a book that is easy to read; sentences which run on for thirteen lines, or in some cases for twenty-seven, become involved in their construction, and the thought which finishes the sentence is far removed from the one which initiated it. One feels that the psychiatrist is apt to indulge in words that singly are significant, but which when put together, psychiatrically at least, convey little even to a trained mind.

Psychiatry is praised as the one field of medicine in which the individual is treated as a whole; he ceases to be his symptoms, and becomes a sick person. Some of this praise is well merited; but the reader cannot help wishing that some of the same scientific atmosphere pervaded the study of psychiatry and its applications as is found in other fields of medical research. We demand rigidly controlled experiments in science but in psychiatry any supposedly peculiar mental reaction is seized upon to explain physical phenomena, but such mental reactions would prove upon investigation to be present in many persons who had no corresponding physical reactions. Also the physical reactions would prove to be present in many who had not suffered the supposedly peculiar mental condition. But having assumed that the simultaneous presence of the two conditions indicates a cause and effect sequence in one case, which assumption may or may not be correct, the same argument of *ad hoc, ergo propter hoc* is erroneously applied to other physical cases.

This example is chosen from the book, and illustrates how this type of reasoning may much mislead one. The author relates the story of a young woman who became pregnant. She rebelled against the idea of the inconvenience, the responsibilities, the loss of freedom which the pregnancy entailed. Hence she developed nausea, vomiting, had a long and serious labor, and was unable to nurse her

*White, William A., *Forty Years of Psychiatry*. Pages, 144. Price, $4.00. Nervous and Mental Disease Publishing Co., N. Y. and Washington, 1933.

child. The question was asked in the book, "Is it not possible to explain all these phenomena simply, rather than to seek in the disturbances of metabolism and organ function and diet and general health and constitution and predisposition, and all the other places that are familiar to us, for causes?" Then the psychiatrist interrogates the "Unconscious," and finds that this woman did not want to become pregnant, that she had planned a trip around the world, and so the Unconscious helps to produce all these untoward effects.

Now it undoubtedly is true that some or all of these physical reactions are present in some women, not through metabolic disturbances but under the aegis of the Unconscious. But what about the woman who deliberately planned her pregnancy, who did not resent the ungainly appearance, nor mind the loss of freedom, but who nevertheless is violently ill during the pregnancy and has a difficult labor? And what about the individual who did not want the pregnancy, but went through it with no disturbance whatever? It is possible to explain all these phenomena "simply" as due to psychical causes, and the great danger is that the profession will become too mentally lazy to find out the underlying metabolic disturbances, and will explain the illness on just such mental grounds. I recall one brilliant woman who almost lost her life under just such a "simple" explanation on the part of her obstetrician. Until we have rigidly excluded all physical causes we should not accept the Unconscious as the etiological factor in disease, although fully recognizing that emotional background must be evaluated sanely as a part of the diseased mechnism.

It is when one turns to the chapter that deals with the modern mental hospital that one wonders just how far this care of the mentally ill is going to carry us. Remembering that the cost of such hospitals is largely state borne, and that many of the mentally ill despite our best care will never be anything but mentally ill, we wonder when the community will begin to care for the physically ill, who can be returned to the community as useful members, as adequately as they care for the mentally ill. The author of the book urges for the care of the mentally ill medical and surgical centers where the acutely ill may be cared for, hospitals for the chronically ill who need rest, laboratories for blood chemistry, X-rays, serology, etc., dietitians to prepare correct diets for the nephritics and the diabetics, and the epileptics; most of the cost of course to be paid by the public.

One cannot help contrasting this ideal, much of which is already realized in the larger mental hospitals, with the hospital for the individual who has never had the misfortune to have trouble with his Unconscious. No such expensive treatment awaits him when he becomes ill. He has to pay his hospital bill, and if he needs special nursing he pays for it. If he needs a surgeon, he pays for him too; no beneficent government steps in to pay his bill. He can only avoid it if the surgeon loses his fee.

Finally the book looks to the future. It is to be expected perhaps, that the psychiatrist in charge of a hospital hopes for bigger and better institutions, with more and more adequate care for the mental patient; but the reader, who is thinking of the portion of the community mentally stable enough not to require institutional treatment, wonders just how long the public purse will stand the expense. When we read such sweeping statements as "there is no existing information, so far as I know, that warrants sterilization as a solution of this problem" and that where sterilization laws are enforced "they are enforced by individuals who are in no position to know anything of the scientific statements of the problem" we feel that prejudice, not reason speaks. Entirely apart from one's

own convictions in the matter, there are certain indisputable facts about which there can be no argument. One should like to see such facts given due weight. Thus with respect to the sterilization of mental defectives—either the type of mental defect under consideration is or is not hereditary. Environment may enhance it, even if hereditary, but it cannot produce the defect if it be primarily an inherited one. Then if hereditary, there is only one way to reduce its incidence, by keeping the affected ones from reproducing, and keep those who are normal themselves but have already produced one defective from producing more. This will not eliminate all defectives but will materially reduce their percentage in the population. This holds true no matter whether the defect is a dominant or a recessive one. This statement is not based upon impressions, but can be demonstrated by mathematical formulae. Quarantining and vaccinating against small-pox have not eliminated it but they have changed it from a world-wide terror to an almost forgotten disease.

If mental defects are not hereditary, then sterilization will not solve the problem as outlined above. But if the psychiatrist is correct in his assumptions that mental twists and psychic trauma received in childhood are responsible for many of the mental disorders, then sterilization would help solve the problem. Surely no mentally defective person, whether feeble-minded or mentally ill, is capable of producing that atmosphere of normality which is to confer on the children of tomorrow that sense of balance which is to enable them to walk the mental tight rope without slipping. No one would maintain, least of all the psychiatrists, that those who have not been able to make their own Unconscious behave are capable of so instructing their children that they in turn will be led into ways of sanity and paths of mental peace. Preventing such mentally ill persons who are still in the reproductive period from procreation should, if the psychiatrist is correct in his assumptions concerning the etiology of mental distances, materially l o w e r their incidence in the coming generations. The last forty years have shown a laudable change in our attitude toward the mentally ill, perhaps the next forty will see the genetic training of psychiatrists which will enable them to balance more equitably the relative effects of heredity and environment.

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BACKGROUND OF SEX EDUCATION

DR. RICHMOND, a clinical psychologist, here presents a broad background of biology, anthropology, history, sociology, psychology, economics, and education.* Obviously, most of these subjects can receive only a passing notice—thus heredity is "covered" in a few pages and some diagrams. Yet the book has at least the advantage of showing the reader that there is something to be known, and he can inquire further if he desires details. While there is plenty of room for difference of opinion in such a large territory, the work is relatively free from serious errors. Its general tone might be described as conservative and constructive.

PAUL POPENOE.

*RICHMOND, WINIFRED, *An Introduction to Sex Education.* Farrar & Rinehart, New York, 1934.

COLOR INHERITANCE IN GALLOWAY-HOLSTEIN CROSSES

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Kansas Agricultural Experiment Station, Manhattan

IN the course of a project carried on at the Alaska Agricultural Experiment Stations some observations were made concerning genetic factors involved in crosses between the Galloway and Holstein breeds of cattle. These observations contain considerable new material bearing on the still somewhat controversial subject of inheritance of color in cattle. The project had as its object the production of a hardy dairy cow for the northern agricultural lands of Alaska. It was begun in 1917 at Kodiak with the reciprocal crossing of hardy Galloway beef cattle and Holstein dairy cattle. The work was carried on at that station until 1926, when the herds were transferred to the interior Alaska station at Matanuska, where the work was continued until its termination in 1932.

Considerable progress had been made in evolving a hardy dairy cow before the work was discontinued as a federal project. The original Holstein dams were mediocre cows, producing 5,000-8,000 pounds of milk. The parent Galloways produced less milk than the Holsteins but it contained from 4 to 6 per cent butterfat. A number of cows and heifers of the F_2 and F_3 generations, giving 10,000 to 14,500 pounds of milk testing 4 per cent fat and more, were being milked at the time the project was abandoned. This amount of milk was nearly twice that of the highest producing parental dams, while the percentage of fat was intermediate between that of the two parent breeds. The ability of the hybrids to withstand low temperatures was also intermediate.

The problem as originally outlined was purely a practical one in which no provision had been made to obtain detailed data concerning the numerous genetic factors involved. However, considerable material was obtained from the routine records, and to these are added observations and data taken by the senior author on his own responsibility during the thirteen years he was Senior Animal Husbandman in charge of the experiment. While the data are taken from the animals and records of the United States Department of Agriculture, the authors assume full responsibility for their correctness, and for the interpretations and conclusions made therefrom.

Foundation Stock

The question of color inheritance only will be considered in this paper. In order to make the presentation more intelligible it seems advisable to give some details regarding the color of the pure breeds that constituted the foundation stock.

In the United States the Galloway breed is considered to be solid black in color. Gourley[2] points out that in its native Scotland it was formerly of various colors, but now only black animals are bred. While a limited amount of white in the inguinal region and along the underline is permitted in animals registered in the Galloway herdbook, animals carrying more than this amount supposedly are barred from registry. However, there cannot be any strict enforcement of the rule since the breeders are not required to indicate the location and the amount of the white (Figures 6, 7, 8, 9, 10, 11).

Holstein breeders deem it highly desirable that their black-and-white cat-

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Figure 6

Galloway bull No. 303, Ranger of Seven Oaks, Reg. No. 45044. He has a few white hairs on the scrotum (*In*) and is a heterozygous self (*Ss*).

Figure 7

Galloway bull No. 329, Aberdeen, Canadian Reg. No. 2646. He has a large amount of white in the inguinal region (*In*) and is a heterozygous self (*Ss*).

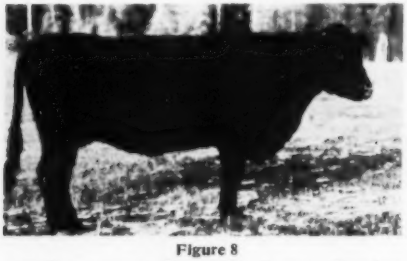


Figure 8

Galloway cow No. 277, Jaynes Banshee, Reg. No. 48193.

Figure 9

Galloway cow No. 215, Fidelia 6th of Kodiak, Reg. No. 41730. She is a solid black (*S, inin*).

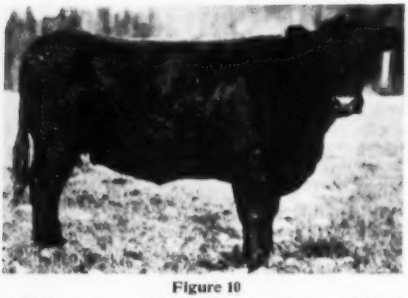


Figure 10

Galloway cow No. 247, True Beauty 3rd of Kodiak, Reg. No. 45138. She has a fairly large amount of inguinal white (*In*) and is a heterozygous self (*Ss*).

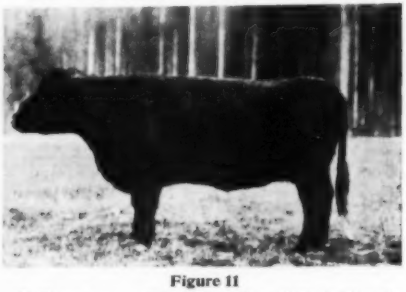


Figure 11

Galloway cow No. 293, Miss of Red Cloud's Girl, Reg. No. 48148. She is entirely self black (*inin*), but is also a heterozygous self (*Ss*). See Figure 17.

SOME OF THE GALLOWAY PARENTS

Formerly the Galloway Breed was of various colors but today only black animals may be registered, with the exception that a little white along the underline is permitted. Color in Galloways is considered to be chiefly controlled by three genes—*B*, black, epistatic to red; *S*, self (complete pigmentation), dominant to white-spotting, *s*. The dominant *In* gene produces white-spotting only in the inguinal region. The Galloways showing spotting in this region carry this gene, the solid color individuals carry the recessive allelomorph, *in*.

Figure 12

Holstein bull No. 1H, Chimacum Sir Quirinus Cornucopia, Reg. No. 176468. Judging from his appearance he would be of the composition *LwlwW*. He is also *plpl*.

Figure 13

Holstein bull No. 20H, Shadford Segis Hartog 2nd, Reg. No. 352564. His composition is probably *LwLw*, although there is also the possibility that he may have a composition such as *LwlwWrwr*. There is much to be learned concerning the interaction of the above genes.

Figure 14

Holstein cow No. 4H, Miss Gladys Cornucopia, Reg. No. 336455. Her composition apparently is *LwLwplpl*.

Figure 15

Holstein cow No. 9H, Gladys Mercedes Banks 2nd, Reg. No. 596282. This animal is probably *LwLwplpl* despite the pigmented spot on the left hind leg. It is not known whether the spot has a genetic basis.

SOME OF THE HOLSTEIN PARENTS OF THE CROSS

Typical Holsteins are homozygous for the dominant black gene and the recessive white-spotting gene. They also carry genes which control the degree of white-spotting, such as the *Lw* gene and its allelomorph. In addition, they lack the pigmented-leg gene, *Pl*, which causes pigmentation to occur below the knees and directly above the hoofs in *ss* animals.

tle carry a considerable amount of white, especially on the legs and underline, with smaller amounts on the head, forming a star or blaze, and on the tail, producing a white switch. No definite pattern is required, but the ideal distribution according to most breeders consists of about equal amounts of white and black, with the pigmented spots being rather large and at the same time fairly regular in outline. Some strains of the breed, however, are practically all white,[1] while others are almost entirely black except for white legs and underline. The breeder, as a rule, has less objection to much white than to much black in his animals. However, the Alaskan Holsteins were generally characterized by a predominance of black (Figures 12, 13,

14, 15). A number of them had but little white above the underline, except for the switch and tongue, which were white in all cases.

The Holstein animals were purchased from various breeders on the Pacific coast. Those with much black were purposely selected inasmuch as it was assumed that this would facilitate the production of the new breed, which was to be self black. Moreover, funds allowed for the purchase of the herd were limited and it was believed that Holsteins carrying much black, of equal quality in other respects, could be purchased for less than could animals carrying the desirable amount of white.

Color Genes

In the present paper no attempt will be made to describe the results of other crossbreeding experiments, nor to give a complete historical account of the discovery of the various genes concerned. It seems advisable only to describe these genes and to indicate them by means of symbols. The descriptions and symbols will be those suggested by Ibsen.[4]

The latter assumes that red (*R*) is always present in the homozygous condition, but that it does not always express itself, due to the fact that other genes, particularly black (*B*), are epistatic to it. An entirely pigmented animal, a self, carries a dominant gene, *S*, which is allelomorphic to *s*, white-spotting. Holsteins are of the composition *ss*. A certain form of white-spotting found only in the inguinal region is due to a dominant gene, *In*. It is epistatic to self (*S*.) Therefore a *SS InIn* animal should be entirely pigmented except for the inguinal white. Up to the present *In* has been reported as being present in only one self breed, the Aberdeen Angus.[3]

Recessive white-spotting (*s*), has a number of modifiers. One of these, *Lw* (little white), is incompletely dominant to its allelomorph, *lw*. Thus a *LwLw* animal has a comparatively small amount of white, a *Lwlw* an intermediate, and a *lwlw* a very large amount. The white-spotting does not form any definite pattern, although there is some degree of regularity in its distribution. It is not always possible to determine with certainty by inspection to which of the above three classes a particular animal may belong.

Another modifier of *s* has been called "pigmented-leg."[5] The pigmented-leg gene, *Pl*, causes pigment to form on the posterior part of the legs below the knees and to extend upward from the hoofs. Animals lacking this dominant gene, and therefore of the composition *ss plpl*, usually are entirely white from the knees downward. Holsteins as a breed have this genetic make-up. A third pair of modifiers (*Wr*, white restriction; *wr*, non-restriction), which has not received much consideration hitherto, will be discussed in the body of the paper.

All typical registered Galloways are black (*B*), and, if they are not entirely self (*S*), they have a small amount of white in the inguinal region (*In*). If all Galloways were homozygous there would be but two genotypes, *BB SS inin* and *BB SS InIn*, so far as the above three genes and their allelomorphs are concerned. Typical Holsteins are *BB ss*, and, according to Gowen, may or may not carry *In*.

The self gene, *S*, is epistatic to all modifiers of white-spotting (*s*). Therefore, if no outcross were made, it would be possible for purebred self Galloways to carry these modifiers indefinitely without their presence being known. By crossing with Holsteins, however, the identity of the modifiers has been made evident in the F_1 (where the Galloways happened to be heterozygous selfs, *Ss*), and in F_2, and later generations.

Heterozygous Self Galloways

Before discussing these modifiers it seems advisable to demonstrate first that some purebred Galloways are heterozygous selfs (*Ss*), and, in addition, to present data showing that there is a single factor difference between the

self of Galloways and the white-spotting of Holsteins.

The proof that some purebred Galloways are heterozygous selfs has been obtained mostly from crosses with Holsteins. In the Alaskan Galloways there is only one record of two purebred animals of this breed, when mated to each other, producing a recessive white-spotted offspring. The male parent, No. 329 (Figure 7) and the female parent both had a rather large amount of white in the inguinal region. The white-spotted (*s*) offspring, No. 349, on the other hand, had a full white underline, an unpigmented tongue, and a white-tipped switch.

Compared to typical Holsteins, however, No. 349, described above, had a very small amount of white-spotting, and the question arises whether there was any justification in classifying it as a *ss* animal. One possibility that could be advanced is that it carried both *S* and *In*, and that plus modifiers greatly increased the amount of white, causing it to be extended forward from the inguinal region. The objection to this explanation is that animals like No. 349, when mated to known *ss* individuals, produced nothing but *ss* offspring. The senior author has also observed that purebred Galloways showing typical inguinal white (*In*) always have black tongues, while all known *ss* animals that have been examined by Ibsen and Riddell have unpigmented tongues. Gowen, however, describes a purebred Ayrshire with a black tongue. The fact that female No. 349 had an unpigmented tongue was the chief reason originally for classifying her as *ss*.

Several matings were made between heterozygous self Galloways and typical white-spotted Holsteins. For example, when the purebred Galloway bull, No. 303 (Figure 6), with a small number of white hairs on the scrotum, was mated to five Holstein cows, three of the five calves were *ss*. One of these calves was No. 14 (Figure 16). It will be noted that the latter, like No. 349 already mentioned and like other calves about to be mentioned, had only a small amount of white. An explanation for this fact will be offered after the results of the other crosses involving purebred heterozygous selfs have been presented.

The Galloway cow No. 247 (Figure 10), with a fairly large amount of white in the inguinal region, was mated to the Holstein bull 1H (Figure 12). The resulting calf, No. 11, had a white underline, switch and tongue. The completely self black Galloway cow No. 293 (Figure 11), also mated to the Holstein bull 1H, produced the *ss* calf No. 18 (Figure 17), with the usual amount of white. The last mating demonstrates that heterozygous selfs, i. e., cow No. 293, need not necessarily show any white, and therefore that *S* is probably completely dominant to *s*, the white that shows in some of the heterozygous being due to *In*.

Sufficient evidence has been given to prove that at least five of the Alaskan Galloways, two bulls and three cows, were heterozygous selfs. None of the others was tested sufficiently to determine whether they were either homozygous or heterozygous. If the above herd is a representative sample of the breed, there is justification for assuming that *Ss* animals are comparatively common.

The prevalence of these heterozygous selfs in the breed can be explained. In the first place, the fact that inguinal white (*In*) is permissible has accustomed the breeders to having some white on their animals. Those *ss* animals that had a large amount of white probably would in most cases be discarded, but others, that had what seemed to be only a forward extension of inguinal white, oftentimes would be retained for breeding. There would be no difficulty in registering these animals since there is no requirement that the location of the white be indicated on the registration blank. On the other hand, they would be under a handicap in the show ring because of the excessive white, and they usually would not be shown.

By retaining for breeding purposes self animals that either did or did not show inguinal white, and only those *ss*

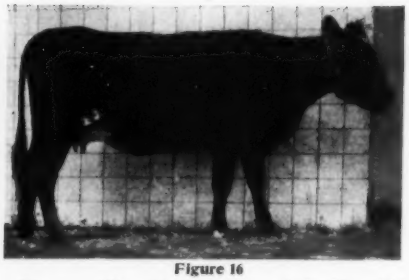


Figure 16

F_1 cow No. 14 [Galloway bull No. 303 (Figure 6) × Holstein cow No. 6H]. The small amount of white on the feet, underline, switch and head, and the unpigmented tongue, characterize her as a *ssWrwr* animal which is probably also *LwlwL*. Her white feet indicate that she is *plpl*.

Figure 17

F_1 cow No. 18 [Holstein bull No. 1H (Figure 12) × Galloway cow No. 293 (Figure 11)]. She is a typical *ssWrwr* animal which probably also is *Pl*. The presence of the latter gene could be determined positively if there were small white spots anteriorly on the lower part of the legs.

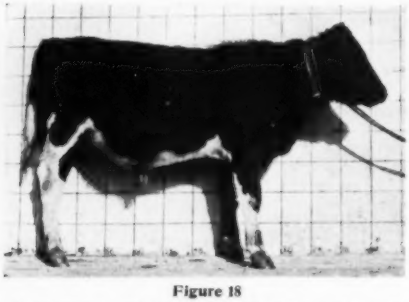


Figure 18

Backcross bull No. 35[Holstein bull No. 20H (Figure 13) × F_1 cow No. 21]. The most probable composition is *ssLwLwwrwrplpl*.

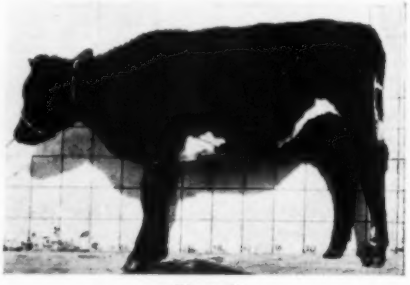


Figure 19

Backcross cow No. 36 [Holstein bull No. 20H (Figure 13) × F_1 cow No. 5]. Postulated composition, *ssLwLwWrwrPlpl*.

Figure 20

Backcross bull No. 12 [Holstein bull No. 7H × F_1 cow No. 1]. This animal has an unusual distribution of white and black on the body. No satisfactory genetic explanation for this phenomenon can be offered at present. It is evident, however, that he carries the pigmented-leg gene, *Pl*. Besides causing the lower legs to be pigmented (except for the small anterior white spots), *Pl* also is responsible for the decrease in size, causing an irregularity in outline, of the white blaze on the head. Note the pigmented flecks in the white spots. The inheritance of such flecking has not as yet been studied.

Figure 21

F_2 bull No. 74 [F_1 bull No. 33 (*Ss*) × F_1 cow No. 14 (*ss*) (Figure 16)]. The most probable composition for this animal is *ssLwlwwrwrplpl*.

Figure 23

F_2 cow No. 31 [F_1 bull No. 6 × F_1 cow No. 3]. This animal is of interest because of her close resemblance to a self (*S*) carrying inguinal white (*In*). She has been classified as white-spotted (*s*), and carrying the white-restricting modifier (*Wr*), chiefly because she has an unpigmented tongue in addition to the white udder and switch. Purebred Galloways with as little white as this animal would probably be kept for breeding purposes, and would tend to increase the number of heterozygous selfs (*Ss*) and also to distribute more widely the *Wr* gene.

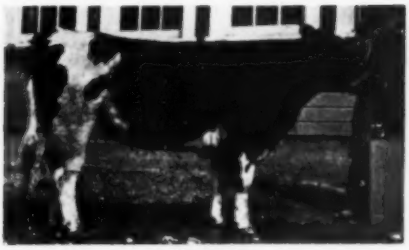


Figure 22

F_2 cow No. 94 [F_1 bull No. 66 × F_1 cow No. 16]. This animal has a comparatively large amount of white for a typical *ssLwLwwrwr* and a small amount for a heterozygote (*ssLwlwwrwr*). At present it is not known what would be the appearance of an animal of the composition *sslwlwWrwr*. There is no question, however, but that she is *plpl*.

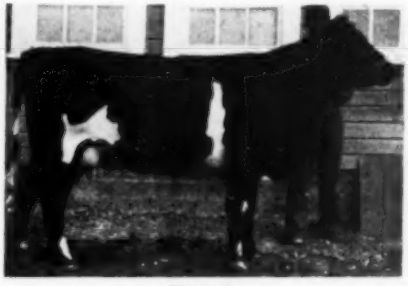


Figure 24

F_2 cow No. 82 [F_1 bull No. 66 × F_1 cow No. 16]. Full sister of No. 94 (Figure 22). She differs from No. 94 chiefly in that she is pigmented-legged (*Pl*).

F_2 AND BACKCROSS ANIMALS

In the second generation *ss* animals appeared with more white spotting than the average Holstein (Figure 21) and with almost as much pigment as a Galloway (Figure 23).

individuals in which the white was greatly restricted, it would follow that many of the selfs would be heterozygous, that the recessive white-spotted animals would tend to show only a small amount of white, and that the selfs would carry white-restriction modifiers of *s*.

Whether or not the above explanation is correct, the fact remains that many purebred Galloways are heterozygous selfs and that the breed as a whole carries modifiers which restrict the amount of white in *ss* animals. It is these modifiers that will now be taken into consideration.

Animals of the composition *ss LwLw* have a small amount of white. How

small can not be stated with exactitude at present, but it is probably true that the typical purebred Guernsey, with a white underline and with a small amount of white on the back, feet, switch and head is of this composition. As was pointed out by Ibsen[4], there is reason for believing that purebred Shorthorns carry another dominant modifier of *s* which causes a further reduction of white. Such animals have the white restricted mostly to the underline, with small amounts on the switch and feet. The purebred *ss* Galloway (No. 349) and the several F_1 *ss* individuals herein reported have approximately this distribution and amount, and the modifier (or modifiers) producing it also acts as a dominant.

Wr Modifier of Recessive White-Spotting

Shorthorn-Hereford crossbreds often have entirely red necks, and Ibsen has postulated that the dominant gene (*Rn*), which according to Miss Pitt[6] causes "red-neck" in purebred Herefords, is identical with the dominant gene (or genes) which reduces the white in purebred Shorthorns, and which we now assume also has a similar effect in Galloways. Under the circumstances it seems advisable to use a new symbol for the modifier, taking for granted at present that there is only one. The symbol suggested is *Wr* (white reducer). It is preferable to *Rn* in that it has a wider significance.

The evidence, so far as it goes, indicates that *Wr* is completely dominant to its allelomorph. It is based on the fact that the purebred white-spotted Galloway described above, presumably homozygous for *Wr*, showed approximately the same amount of white as the white-spotted Galloway-Holstein F_1 animals, presumably heterozygous for this gene.

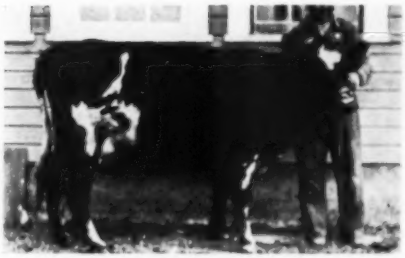
Taking the above genes into consideration, a typical Guernsey should be *ss LwLw wrwr*, while a typical Shorthorn or a white-spotted (*ss*) Galloway should be *ss* (*LwLw*) *WrWr*. There is no direct evidence at present as to whether or not Shorthorns or Galloways are *LwLw*, but the interpretation given here, until further evidence accumulates, is that *Lw* and *Wr* are, to a large extent at least, duplicates of each other and that their action is cumulative.

By assuming the above interpretation in regard to the interactions of *Wr* and *Lw* one can devise an explanation for the occasional occurrence of purebred Holsteins showing an exceedingly small amount of white. It would have to be assumed that *Wr* and *Lw* are both present in the breed, and that, by constant selection against animals having too little white, *Wr* gradually is being eliminated, the reverse being true in the Shorthorn and Galloway breeds. However, when *Wr* and *Lw* are both present in the same animal, and especially in one that is homozygous for *Lw*, the amount of white is assumed to be exceptionally small.

Self (*S*) and White-Spotting (*s*)

It has been taken for granted for many years that self and white-spotting are allelomorphs, but so far as we can determine the evidence is based mostly on the fact that F_1 animals are selfs and that two selfs occasionally produce a white-spotted offspring. For this reason it seems advisable to present the ratios that were obtained when heterozygous selfs were mated either to white-spotted individuals or to other heterozygous selfs.

There were various kinds of heterozygous selfs used in the matings with the white-spotted Holsteins. For example, the purebred Galloway bull 303 (Figure 6) mated to purebred Holsteins, produced two self and three white-spotted offspring (Figure 16). Two purebred Galloway cows, mated to purebred Holstein bulls, each had only one calf, in this case a white-spotted one (Figure 17). The *ss* calves from all of the above matings showed the *Wr* modifying gene carried by Galloways. Holstein-Galloway F_1 self males mated to Holstein cows sired



A HIGHLY PIGMENTED F_2 AND A RED CROSSBRED

Figure 25

F_2 cow No. 88 [F_2 bull No. 69 × F_2 cow No. 65]. She shows the pigmented leg (*Pl*) character contributed by the purebred P_1 Galloways. The effect of *Pl* on the white blaze is also shown. In this particular animal one gets the impression that the *Pl* gene has also caused some pigmented blotches to appear in the white area on the side of the body.

Figure 26

Self red cow, B [F_2 bull No. 46 × F_1 cow No. 39]. She is the only red animal produced among the purebred Galloway and Holstein herds and their crossbred descendants. No white hairs are present (*S inin*).

three self and three white-spotted animals, and in the reciprocal mating there were three self and four white-spotted offspring (Figures 18, 19, 20). A number of the Galloway-Holstein F_1 white-spotted (*ss*) cows were mated to F_1 self bulls. The offspring consisted of five self and three white-spotted animals (Figure 21). Finally, a heterozygous self F_2 bull (No. 46) produced one self and three white-spotted animals when mated to F_2 white-spotted cows. The total offspring from the above matings were fourteen selfs and eighteen white-spotted, a reasonably close approximation to the theoretical 1:1 ratio.

The heterozygous selfs mated to each other were almost entirely F_1 animals. The offspring, where both parents were F_1 selfs, consisted of fifteen self and six white-spotted individuals (Figures 22, 23, 24). In addition, the F_2 bull, No. 46, mentioned above, and shown to be a heterozygous self, sired three self calves when mated to self F_1 cows. The combined results are eighteen selfs and six white-spotted, a perfect 3:1 ratio.

It should be noted that, both in the back-cross of heterozygous selfs to white-spotted and in the mating of heterozygous selfs to each other, there were white-spotted offspring produced that had a considerable amount of white (Figures 20, 21, 22). These probably were animals that lacked the white-restriction modifier, *Wr*, contributed by the ancestral purebred Galloways.

Pigmented-Leg (*Pl*) in Galloways

The pigmented-leg gene comes into expression in *ss* animals, but does not show in selfs (*S*). Purebred Holsteins are, with few exceptions, entirely white below the knees. Even the exceptions, however, do not carry *Pl*. Therefore, if pigmented-leg shows among the *ss* descendants of the Holstein-Galloway cross, the gene must have come from the purebred Galloways. Several examples will be cited.

The first individual to show pigmented-leg was the back-cross male calf No. 12 (Figure 20). His sire was the purebred Holstein bull 7H, and his dam the Galloway-Holstein F_1 cow No. 1. Another *Pl* animal produced by a similar back-cross was No. 36 (Figure 19). Several of these animals occurred in the F_2 generation, as for example, ♀ 82 (Figure 24), and in the F_2 generation, ♀ 88 (Figure 25). It will

be noted in these pigmented-legged animals that wherever white is present on the legs it is located anteriorly, and that the *Pl* gene also causes an irregularity in the outline of the white blaze on the head (Figures 20 and 25).

Occurrence of Red

Both of the parent breeds in the experiment carried black (*B*). In neither of the purebred herds nor in any of the F_1 animals did a red individual (*bb*) occur. One was produced, however, when an F_2 bull (No. 46) was mated to an F_1 cow (No. 39). This animal (Figure 26) was of a deep cherry red color, with brown nose and tongue, and showed no white hairs whatever.

The parents of the red calf were entirely unrelated so far as our records go. Although red calves are known to occur in both of the pure breeds, the calf above mentioned was the only red one among the more than 500 animals raised in the Alaskan experiment.

Summary

1. The dominant gene, *In*, causing white in the inguinal region, is present in purebred Galloways.

2. Proof is furnished that a comparatively large number of purebred Galloways are heterozygous selfs (*Ss*). An explanation for this fact is suggested.

3. Data are presented, mostly from Galloway-Holstein crosses, showing the one-factor, allelomorphic, relation of self (*S*) to recessive white-spotting (*s*).

4. It is shown that purebred Galloways carry two dominant modifiers of *s*. One of these, *Wr* (white-restricter), is present in most animals, while the other, *Pl* (pigmented-leg), is comparatively more rare.

5. By means of *Wr* an explanation is offered for the occasional occurrence of purebred Holsteins which are to a very large extent devoid of white-spotting.

6. In the Galloway-Holstein cross a red (*bb*) calf was produced from the mating of an F_2 bull to an F_1 cow, thus furnishing evidence that at least one of the purebred ancestors was a heterozygous black (*Bb*).

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Woolly Haired Horses

THE recent articles on woolly haired mutations in men, cattle, and swine have elicited comment from one of our members in the Argentine, Mr. Richard Hogg, regarding a woolly strain of horses. These were common enough half a century ago so that they were given a name (Crespos). The Crespos were not a breed apart but occasionally appeared in the big herds on some of the larger ranches in the region south of Buenos Aires. Subsequently they apparently have died out. They were of all colors, but were of a characteristic stocky build. Possibly the climate has led to the survival of some of these horses in some other region. It was believed that the semi-hairless cattle recently reported in this Journal were less viable than the normals and such a reduced viability may have also affected the survival of the woolly horses.

A CASE OF CHLOROPHYLL DEFICIENCY IN RICE

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STRIPED, NORMAL AND ALBINO RICE SEEDLINGS
Figure 27

Segregation of striped and albino seedlings in a ratio of 63 normal to 1 striped indicates that this type of chlorophyl deficiency is governed by three recessive factors. Two of these factors are carried by varieties which have been grown in British Guiana for many years, but produce no effect in the absence of the third, which was contributed by certain American varieties. In order for these mutations to be made manifest it is necessary that they be brought together from the widely separated regions in which they have occurred.

AMONG the F_2 progenies of several crosses made at the Experiment Station, Georgetown, British Guiana, between local and American varieties of rice, a small number of chlorophyll deficient seedlings was obtained, the deficiency manifesting itself by the production of white and striped seedlings. This is extremely unfavourable from the economic point of view because, apart from the lethal or semi-lethal effect of the homozygous condition, it has been shown[5] that plants heterozygous for such a character may be less vigorous than homozygous green plants. This is supported by Mangelsdorf[6] who studied the effects of two lethal recessive seed factors on the height of maize. Normal green plants were found to be tallest; those heterozygous for one factor were slightly shorter, and those

heterozygous for two factors fell into the shortest class.

Materials and Results

One parent, Demerara Creole, used in all the crosses which produced chlorophyll deficient plants, is an improved strain from a variety grown locally for many years. Thus its origin is obscure. Its introduction probably followed the importation of indentured labour from India. The other parents are three American varieties, namely, Mexican Edith, Americano 1600, and Blue Rose.

The technique of hybridization adopted is that described by Chao[1] and Sampietro[8].

All parental types and the F_1 hybrids were normal green in appearance and the F_2 progenies segregated into trihybrid ratios of 63 green : 1 albino. The counts made are shown in Tables I, II and III.

Values for x^2 were obtained from Fisher's data[2].

In each of the above cases the trihybrid ratio is supported by the numbers observed and it is probable that Demerara Creole possesses two of these genes, the third being contributed by the other parents. Ramiah[7] records the appearance of albino plants in various crosses and in one case the F_2 segregated into 15 green : 1 pale yellow. The yellow plants though weak attained maturity.

A small number of striped plants (mentioned previously) has been added to the green class and were distributed as follows:—

Nature of Cross	No. of striped plants
Mexican Edith × Demerara Creole	18
Americano 1600 × Demerara Creole	5
Blue Rose × Demerara Creole	9

These striped plants were of two distinct types, namely:—

(1) Plants with broad green and white stripes running throughout the length of the leaf sheath and blade. These plants rarely survive for longer than 4 or 5 weeks. Sometimes only one tiller is affected and this tiller dies leaving the plant normal green in appearance, suggesting an aberration during somatic mitosis. Chimeras of this type affecting other morphological characters have been described by Ramiah[7] (colour of glumes) and Sampietro[9] (size of grain).

(2) Plants with a thin white stripe along the midrib which broadens slightly as it reaches the tip of the leaf.

TABLE I.—Segregation in the F_2 of the cross Mexican Edith × Demerara Creole.

	Green	Albino	Total	x^2
Observed numbers	2342	43	2385	.895
Expected (63:1 ratio)	2347.73	37.27	2385	

P lies between .5 and .3

TABLE II.—Segregation in the F_2 of the cross Americano 1600 × Demerara Creole.

	Green	Albino	Total	x^2
Observed numbers	1014	17	1031	.04
Expected (63:1 ratio)	1014.89	16.11	1031	

P lies between .9 and .8

TABLE III.—Segregation in the F_2 of the cross Blue Rose × Demerara Creole.

	Green	Albino	Total	x^2
Observed numbers	2542	47	2589	1.07
Expected (63:1 ratio)	2548.55	40.45	2589	

$P = .30$

In these plants all leaves are affected but the plant usually survives. A study of the progeny of these plants, which is at present being undertaken, will throw some light on their origin.

Ikeno[3] refers to an investigation by Takezaki in connection with a variety in which the culm and leaves are striped with white; in this case there was segregation into white, striped and green plants, though the inheritance was non-Mendalian, being transmitted through the maternal cytoplasm.

Kondo, Takeda and Fujimoto[4] describe crosses with similar plants and record the same results.

Figure 27 shows green, striped and white seedlings from the cross Mexican Edith × Demerara Creole. The variety Demerara Creole is pigmented at the base of the leaf-sheath while Mexican Edith is non-pigmented. The presence of pigment which may be observed at the bases of plants 1, 3, and 5 indicates the independent inheritance of chlorophyll inhibitors and anthocyan pigment.

Summary

A case of chlorophyll deficiency is described involving three factors which in the homozygous recessive condition produce white seedlings. It is probable that the variety Demerara Creole possesses two of these factors while the third is contributed by the American varieties, Mexican Edith, Americano 1600 and Blue Rose.

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Chick Sexing Schools In Thirteen States

POULTRYMEN continue to show a lively interest in the sexing of baby chicks, according to H. L. Shrader, extension poultryman of the United States Department of Agriculture, who has been assisting with chick-sexing demonstrations in 13 States during the summer and early fall. (The method was described in the Journal of Heredity 24:67, February, 1934.)

Although such a demonstration is considered one of the best methods of learning how to do this work, some poultrymen have studied the procedure of their own accord with the help of textbooks and other literature. A mimeographed pamphlet which gives the essential directions has been issued by the Department. Copies may be obtained from the Bureau of Animal Industry, United States Department of Agriculture, Washington, D. C.—*U. S. Dept. Agr. Clip Sheet.*

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MILDRED ROSSMAN

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Preliminary Program of Botanical Congress

The Organization Committee of the VI International Botanical Congress, to be held at Amsterdam, September 2-7, 1935, announces that the following topics preliminarily have been chosen for discussion in the sections:

AGR. Agronomy. (1) Interactions between roots and soil; interactions between plants. (2) Virus diseases. (3a) Weed flora as an indicator of soil conditions in agriculture. (3b) Grass land associations. (4a) Genetics and breeding of immune varieties. (4b) Inbreeding. (5) Importance of microbiological investigations in the study of agricultural problems. (6) Influencing the cycle of development in plants.

CYT. Cytology. (1) Structure of chromosomes. (2a) Crossing-over versus conversion. (2b) Terminology of cytology and genetics. (3a) Pairing of chromosomes in polyploids. (3b) Reduction division in fungi. (4) Chain- and ring formation of chromosomes. (5a) Submicroscopical structure of the cellwall. (5b) Vacuome, chondriome, plastids. (6) Colloid chemistry of protoplasm; vital staining.

GEN. Genetics. (1a) Experimental mutations. (1b) Genetical basis of size and form. (2a) Crossing-over versus conversion. (2b) Terminology of cytology and genetics. (3a) Sexuality in fungi. (3b) Reduction division in fungi. (4a) Genetics and breeding of immune varieties. (4b) Inbreeding. (5) Taxonomy and genetics. (6a) Plasm and genotype in their mutual relations. (6b) Letal factors.

GEO. Geobotany, ecology and phyto-geography. (1) Climate associations in N. W. Europe and N. America. (2) Cartography: (a) Vegetation maps; (b) Area maps. (3) Flora and vegetation area. (4) Plant geography in younger formations. (5) The halophyte problem. (6a) Classification and nomenclature of vegetation units. (6b) Miscellaneous papers.

MOR. Morphology and anatomy. (1a) Size and form. (1b) Genetical basis of size and form. (2a) Phytohormones; general paper. (2b) Leaf arrangements. (3) Flower morphology. (4) Female fructification and phylogeny of Conifers. (5a) Wood anatomy. (5b) Relations between anatomy and external morphology. (6) Morphology of Bryophytes.

MYC. Mycology and bacteriology. (1) Differential characters in Hymenomycetes. (2) Nomenclature of fungi. (3a) Sexuality in fungi. (3b) Reduction division in fungi. (4) Biologic forms of fungi. (5) Importance of microbiological investigations in the study of agricultural problems. (6) Phylogeny and taxonomy of Phycomycetes.

PATH. Phytopathology. (1) Biological basis of plant quarantine. (2) Virus diseases. (3) Various papers. (4) Biologic forms of fungi. (5) Immunization. (6) Physiologic diseases.

PB. Palaeobotany. (1) Geobotanical provinces in the older formations. (2) Caytoniales and Pteridospermae and the evolution of Angiosperms. (3) Flower morphology. (4) Plant geography in younger formations. (5) Synchronism and uniformity in palaeozoic and mesozoic floras. (6) Various papers.

PH. Plant physiology. (1) Photosynthesis. (2a) Phytohormones; general paper. (2b) Phytohormones; various papers. (3) Oxidation, reduction and metabolism. (4) Permeability and the accumulation of mineral elements. (5a) Submicroscopical structure of the cellwall. (5b) Translocation of plastic materials. (6) Influencing the cycle of development in plants.

SYS. Taxonomy and nomenclature. (1) Various papers. (2) Caytoniales and Pteridospermae and the evolution of Angiosperms. (3) Flower morphology. (4) Female fructification and phylogeny of Conifers. (5) Taxonomy and genetics. (6) Phylogeny and taxonomy of Phycomycetes.

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A DWARF MUTATION IN THE RAT

A Mendelian Recessive Character Possibly Due to a Defect of One of the Endocrine Glands

W. V. LAMBERT and A. M. SCIUCHETTI
*Iowa State College**

THE dwarf character described herein was first observed in the summer of 1933 in a strain of albino rats that has been maintained in our genetic colony since 1927, and which has been rather closely inbred for the past three years. Shortly after the appearance of the first dwarf individual, another dwarf was observed in a litter produced by a closely related pair. Since then dwarfs have been produced by a number of descendants of these pairs and by other closely related individuals within this strain.

This is the fourth case of dwarfism reported in rodents. The first was reported in 1909 by Sollas[5,6] in the guinea pig, the second by Snell[4] in the mouse, and the third by Greene, Hu and Brown[1] in the rabbit. In only one case has the apparent cause of the dwarfism been determined. Smith and MacDowell[2] pointed out that the drawf mutation in the mouse was due to an hereditary anterior-pituitary deficiency which could be corrected by the daily transplantation of normal rat pituitary glands. In a subsequent report[3] they showed that the mutation caused a suppression of the growth promoting hormone of the pituitary without a corresponding suppression of the gonad stimulating hormone. In the rabbit the mutation is lethal, the evidence indicating that the condition is of endocrine and possibly of pituitary origin. The description of the dwarf character in guinea pigs suggests an achondroplastic type of dwarfism.

Description of the Dwarf Rat

At birth the dwarf rats resemble their normal litter mates and cannot be separated from the normals with any degree of certainty until about the twelfth day after birth. At this age the hair on the dwarfs appears softer, finer and much thinner than on the normals. This condition of the hair is a permanent characteristic, although the most obvious difference in the coat is evident about the fifteenth day. A few of the dwarfs develop no hair till several days after their normal litter mates.

After from twelve to fifteen days the ears can be seen to be larger in proportion to body size than those of normals, the ear size apparently not being reduced in proportion to body size. In body proportions the dwarfs are comparable with the normals, the reduction in size seemingly being general throughout the body, with the possible exception of the ears. No disproportion of the bones has been observed in skeletons of the dwarfs so far examined.

In all dwarfs produced thus far there has been a distinct opacity of the eye, apparently involving the lens. As a result the dwarfs do not see readily, if at all. This opacity is apparent in the dwarfs shown in Figure 28.

The dwarf rats are weaker, much less thrifty, and are shorter lived than their normal litter mates. If they are to be successfully raised they must be isolated from the normals and kept under favorable conditions. The dwarfs show no sexual activity, and all have proven entirely sterile. The testes remain infantile becoming less than one-half normal size. A few spermatozoa were observed in the epididymis and in the testes of one dwarf male, but these were completely immobile in physiological saline solution and their tails were malformed. As yet no examinations of the

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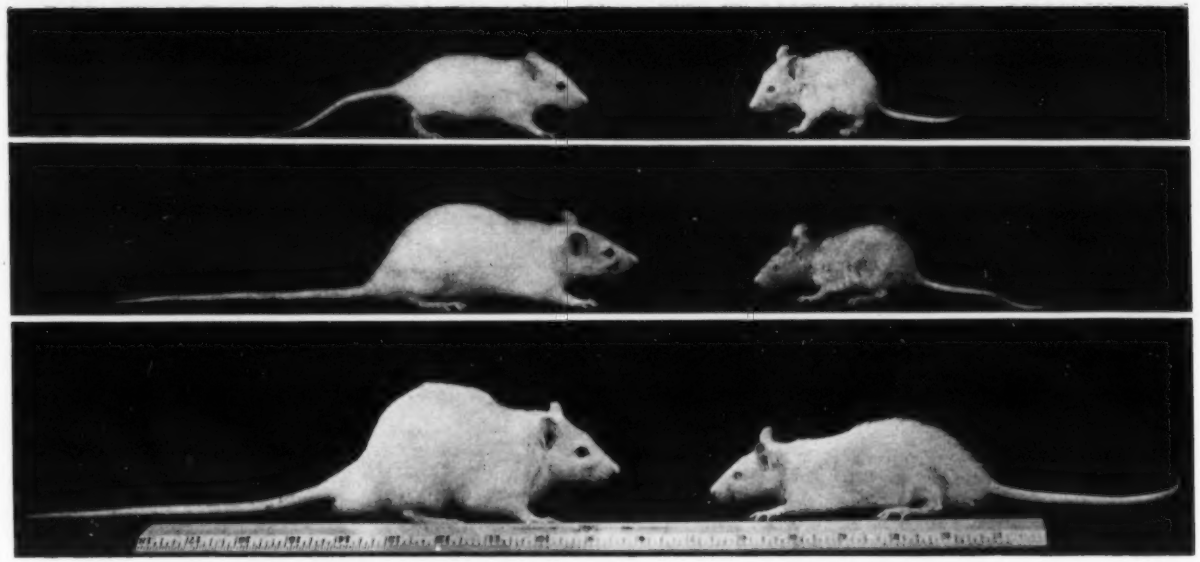


RELATIVE SIZE OF NORMAL AND DWARF RATS AT 27, 52, AND 140 DAYS

Figure 28

A genetic form of dwarfism has been reported in the guinea pig, the mouse, and the rabbit but not heretofore in the rat. At birth dwarf and normal are approximately of the same size and they cannot be differentiated by eye until about the twelfth day although statistical analysis proves that the dwarfs have begun to grow significantly more slowly by the fifth day. Inherited dwarfism in the mouse is due to a failure of the pituitary gland but implantation of pituitary bodies produced no effect in the rat. The condition is apparently governed by a single recessive gene, but the complete sterility of the dwarfs has precluded the direct test of inter-breeding affected individuals.

ovaries have been undertaken.

A remarkable feature of the dwarfs is the failure of males and females to become differentiated in size. Whereas normally the male becomes from 100 to 150 grams heavier than the female, little difference in the adult weight of males and females occurs in the dwarfs. The weights of normal and dwarf litter mates that reached maturity and whose weights are available for comparison are as follows:

	Normal		Dwarf	
	♂	♀	♂	♀
Litter 1	285	203	140	.....
Litter 2	326	210	.....	144
Litter 3	305	.....	151	.....

Figure 28 shows normal and dwarf litter mates at ages of 27, 52, and 140 days. The normal proportion of body parts is evident from these pictures.

Growth of the Dwarf

As previously mentioned, the dwarfs cannot be differentiated at birth from their normal litter mates. In order to determine at what age a size difference became manifest, weights of each animal were taken every four days, beginning on the fifth day after birth in all litters in which dwarfs might be expected to appear. An analysis of variance was made of the weights taken on the fifth day of six litters in which dwarfs appeared. Table I shows the result of this analysis. The total variation, namely the sum of squares, is 39.52. This variation is due to the variation between the six litters, to that between groups within litters and finally to the variation within groups. For this study the variation between means of groups within litters is of most importance. As there are only two groups within one litter only one degree of freedom is left. The ratio of the larger mean square, between means of groups, to the smaller, between means of groups within litters, gives an F value of 21.13, which is highly significant. The decreased rate of growth in the dwarfs, therefore, has begun to manifest itself at an age of five days, although from appearance it is impossible to detect a difference in size until about the twelfth day. Snell in his work with dwarf mice was unable to observe any difference between dwarfs and normals until about the fourteenth day. In this respect the dwarf rat would appear to differ from the dwarf mouse although it is not evident from Snell's description that an analysis of early birth weights was made.

Growth curves of normals and dwarfs to the age of 61 days are presented in Figure 29. These curves are based upon the composite weights of seven dwarfs from two litters (6 and 8) and 13 normals from these same litters. Maximum weight in the dwarfs, as determined on the few dwarfs that have reached maturity, is attained at approximately four months. The mature weight of the dwarfs is about 50 per cent of that of the normal males and approximately 70 per cent of that of the normal females of this strain. No sexual difference occurs in the mature weights of males and females, nor is there a difference in rate of growth between the two sexes.

Inheritance of Dwarfism

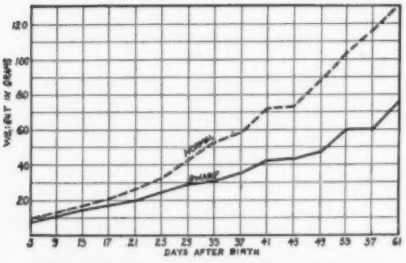
Twelve litters in which dwarfs appeared have been produced. The proportions of normals and dwarfs, and of the males and females in each category are shown in Table II. A total

Table I. The analysis of variance of the weight at the fifth day after birth.

Source of variance	D. F.	Sum of squares	Mean square
Total	50	39,52	0,79
Within groups	39	27,70	0,71
Between means of groups	1	8,03	8,03
Between means of groups within litters	10	3,79	0,38
$F = \frac{8.03}{0.38} = 21.13$			

Table II. The distribution of normal and dwarf rats in twelve litters in which dwarfs have appeared.

Litter No.	Normal rats			Dwarf rats		
	♂♂	♀♀	Total	♂♂	♀♀	Total
51	5	3	8	1	0	1
52	7	3	10	1	0	1
6	4	6	10	1	0	1
8	7	6	13	1	3	4
12	4	5	9	1	1	2
17	4	3	7	1	1	2
18	4	3	7	1	1	2
20	4	3	7	1	0	1
45	3	3	6	0	1	1
48	3	3	6	1	0	1
52	3	4	7	1	0	1
53	0	4	4	0	2	2
Totals	42	38	80	11	11	22



GROWTH CURVES COMPARED

Figure 29

Composite growth curves of seven dwarfs and thirteen normals from two litters. At birth the weights were practically the same but by five days the weight difference between normals and dwarfs had begun to assume statistical significance. There is no sex differentiation in the weight of dwarfs such as characterizes normal rats.

of 102 young were produced in these litters, 80 being normal and 22 dwarf. These results indicate that the dwarf character is dependent for its expression upon the action of a monogenic recessive mutation, the expectation in such a case being 77 to 25. The appearance of both male and female dwarfs definitely precludes a sex-linked mode of inheritance. Three males and ten females have produced these twelve litters, thus indicating that the gene is well distributed among the normal rats of this strain. As proven heterozygous males and females become available the relative proportion of homozygous and heterozygous normals in various litters is being determined. The complete sterility of the dwarf, unfortunately, makes it necessary to work through the heterozygotes.

The general characteristics of these dwarfs, namely the reduced size, the sterility, the decreased activity, the failure of males and females to become differentiated in size, and the generally reduced vigor suggest that the cause is of endocrine origin. However, preliminary experiments involving the transplantation of normal rat pituitary bodies into dwarfs, following the method of Smith and MacDowell, have failed to produce growth or to stimulate sexual activity in the treated dwarfs. These results would indicate that the cause of the dwarfism is not of pituitary origin although this is being subjected to further tests. As dwarfs become available additional experiments are also being carried forward in an effort to determine the physiologic nature of the dwarfism.

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"How Shall We Know Plants?" Accidentally Anonymous

The combined review of Small's *Manual of the Southeastern Flora* and MacBride and Martin's *Myxomycetes* in the January Journal (pp. 25-31) was left unsigned through an editorial blunder. The author was Doctor O. F. Cook of the U. S. Department of Agriculture.

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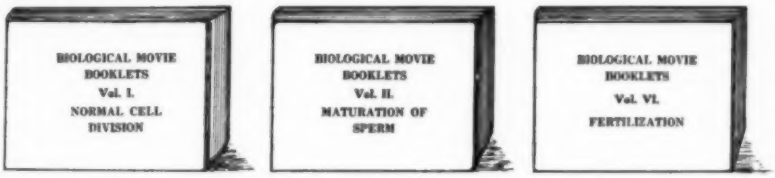

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